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A sedimentological study of Devil's Lair, Western Australia

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Abstract

The sediments in Devil's Lair cave, Western Australia, show a complex sequence of depositional and diagenetic events. Most of the clastic sediments are derived from weathered aeolianite. The main feature of the cave sediments is their textural uniformity, seemingly independent of microclimatic variations; this is inherited from the aeolianite source rock. The clastic sediments are interbedded with complex flowstone layers, formed during sedimentation pauses related to changes of the cave entrance, and are lithified through carbonate cementation. Human or animal activity had little influence on either the composition or the diagenesis of the cave sediments.

Introduction

Devil's Lair is a small cave about 5 km from the sea in Quaternary aeolianite in the Cape Leeuwin-Cape Naturaliste region of the extreme southwest of Australia (Fig. 1). The cave deposits have recently been excavated by members of the staff of the Western Australian Museum, leading to a series of important archaeological and biotic finds which are summarised in the works of Dortch (1974), Dortch and Merrilees (1972, 1973), and Baynes, Merrilees and Porter (1976). The writer studied samples from the 1970 excavations and collected further samples during a visit in April 1974.

General setting

Geology

Devil's Lair cave was formed in the calcareous aeolianite (Tamala Eolianite) capping the Precambrian crystalline rocks that form the Leeuwin-Naturaliste ridge. The mostly lithified dune deposits occur at elevations of up to 230 m, and their distribution is shown in Fig. 1. Although the aeolianite is predominantly a limestone, the calcium carbonate content ranges from 10% to 90%. The calcareous particles consist of sponge spicules, fragments of mollusc shells, calcareous algae and foraminifera. The remainder of the rock consists of quartz, feldspar and heavy minerals. The older dune deposits are cemented by calcium carbonate. Caves are developed in the lithified dunes and these are generally found on the leeward side of the ridge, possibly formed by solution processes acting below the water table (Bastian 1964). The cave systems are complex and interconnecting, and many open out of dolines, as in the case of Devil's Lair and Nannup Cave, which open from the same doline.

Soils

The soil pattern of the coastal dunes varies with erratic and variable segregation within the parent material as a result of leaching, the dominant pedogenetic process. They generally have a superficial layer of dark brown loamy sand, containing some organic matter and sel-

dom more than 6 cm thick, which overlies 6-42 cm of dark brown sand with a little clay, and a further 6 cm of brown sand over the

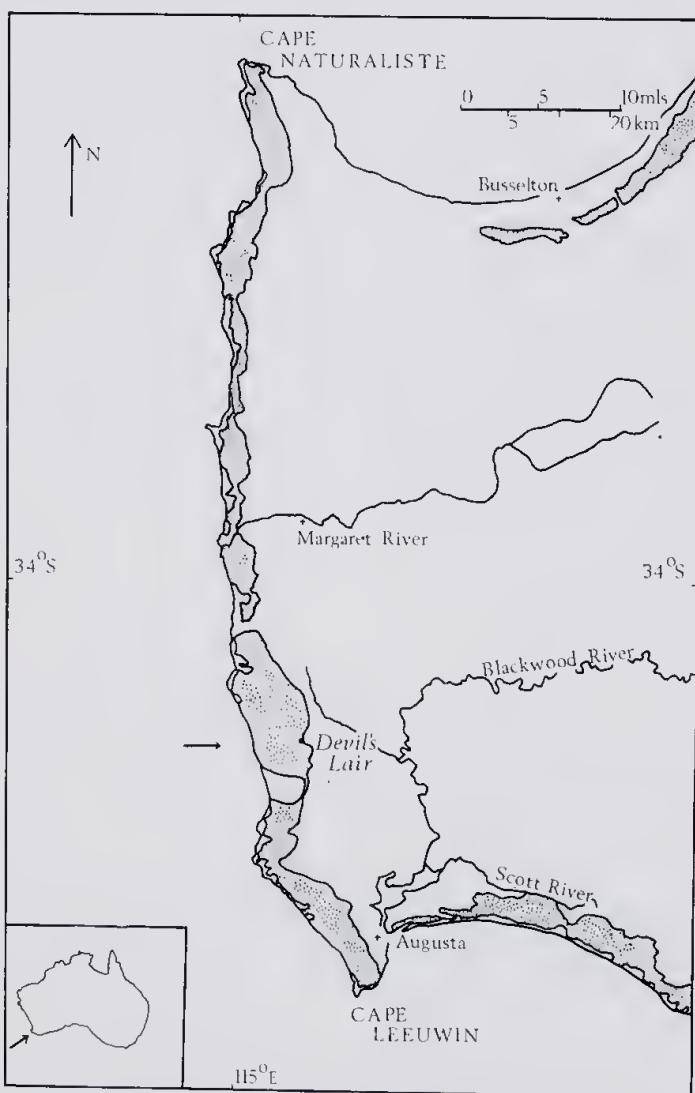


Figure 1.—The Cape Leeuwin-Cape Naturaliste region of Western Australia, showing the location of Devil's Lair. The shaded area represents the approximate distribution of the Tamala Eolianite. Modified from Lowry (1967).

limestone cap rock. Lumps, nodules and bands of ferruginous material are common, and such soils present a marked contrast to the acid podzols which develop further inland.

Climate and vegetation

At present the vicinity of the cave has a high annual rainfall of 910-1520 mm, falling in the winter months, and the vegetation is an open Karri forest (*Eucalyptus diversicolor*) with an understorey including Peppermint (*Agonis flexuosa*). Low woodland, scrub and open heath occur nearer to the coast.

Cave morphology

The cave consists of a single chamber, irregular in shape, with two separate entrances, one of which (the northern) is now blocked by a talus cone composed of clastic deposits and flowstone (see Fig. 2). The southern entrance

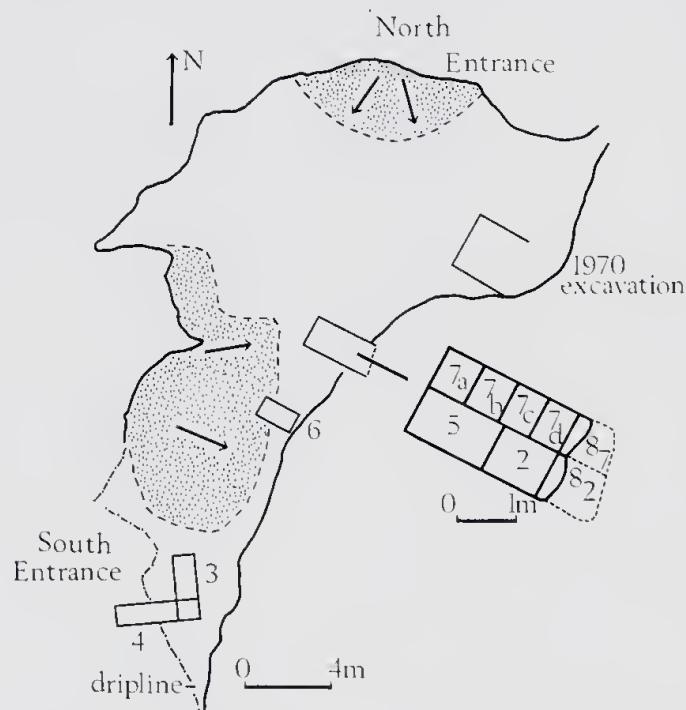


Figure 2.—Sketch plan of the cave floor of Devil's Lair, showing the location of excavation trenches. The shaded areas indicate the approximate extent of the main talus cones.

is the present means of access, but the slope of the strata suggests that it was not open during most of the depositional history of the cave, and that the greater part of the sediments entered from the north.

The floor of the cave is mainly covered by a sheet of flowstone of irregular thickness. Active speleothem formation continues and water still enters the cave through crevices. Cave temperature remains relatively constant and light penetrates into the cave, with the exception of the extreme rear (northern area), more than 15 m from the present entrance.

Clastic sediments

The sediments consist of interbedded sand, flowstone and stalagmite, together with lithified bands and occupation horizons. In places they have been disturbed by animal activity, and the occasional occupation by human groups is evidenced by the presence of hearths and pits. Nonclastic material includes bone, artifacts, charcoal and other biotic remains. The maximum thickness of the sediments is in excess of the 4 m established in the excavation. A radiocarbon date from immediately below the uppermost flowstone which seals the deposits indicates the end of clastic sedimentation shortly before 6490 ± 145 BP. The oldest samples are probably older than 30 000 BP.

Analytical procedures

Trenches 2, 5, 7 a-d, 8 (2) and 8 (7) (Fig 2) were sampled in 1974 for laboratory analysis, together with samples from Trench A1 which were collected in 1971. Dry sieve analysis, grain surface texture studies and determination of chemical composition were carried out in the laboratory (Shackley 1975) to complement the field data. Field observations focussed on description of composition, colour, texture, cementation and compaction. Field tests for pH, phosphates and humus were also carried out.

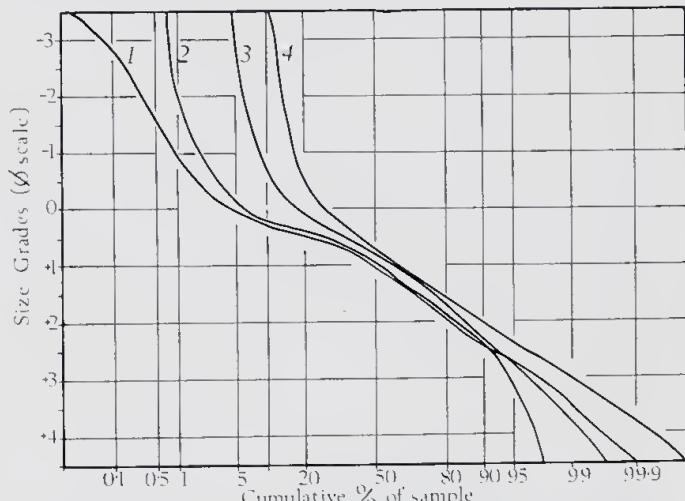


Figure 3.—Particle size distribution curves, plotted on arithmetic probability paper, for samples from Devil's Lair. 1—Low orange brown earthy layer, Trench 6. 2—Middle orange brown earthy layer, Trench 6. 3—High orange brown earthy layer, Trench 6. 4—Trench 6, top first orange brown earthy layer.

Composition

Thirty samples of the clastic sediments, taken from different trenches, were subjected, after decalcification, to a detailed particle size analysis by dry sieving. Table 1 shows that the sediments consist chiefly of rather poorly-sorted gravelly quartz sands, generally positively skewed and leptokurtic. The proportion of mud (silt and clay) in the samples was very low, only 4 samples containing more than 5%. Fourteen

Table 1.
Particle size analysis, Devil's Lair sediments.

Source of Sample	Approx. depth (cm. below cave datum)	Weight processed (g)	Composition			Descriptive Parameters				Textural Description (Folk 1954)
			Gravel (%)	Sand (%)	Mud (%)	Mean (ϕ)	Standard Deviation	Skewness	Kurtosis	
Topsoil outside cave	(above)	878.2	20.5	73.4	5.9	0.69	2.00	0.29	1.06	Gravely sand, moderately sorted, mesokurtic
Tr. 7c, 'Dark earthy layer'	75	1645.0	13.7	85.4	0.7	0.78	1.42	-0.18	1.62	Gravely sand, poorly sorted, very leptokurtic
Tr. 5, 'dark earthy layer'	60	845.0	3.9	89.9	6.1	1.35	1.48	0.32	1.17	Gravely sand, moderately sorted, mesokurtic
Tr. 5 'earthy' band in 'flowstone complex'	80	1230.0	3.7	95.6	0.5	1.07	1.04	-0.29	0.99	Slightly gravelly sand, poorly sorted, mesokurtic
Tr. 5, 'first orange brown earthy layer'	150	1289.0	0.4	99.4	0.0	1.13	0.97	0.36	0.84	Slightly gravelly sand, moderately poorly sorted, platykurtic
Tr. 5, 'light earthy layer'	220	1108.0	6.4	92.8	0.7	0.78	1.01	0.03	1.66	Gravely sand, poorly sorted, mesokurtic
Tr. 5, 'second orange brown earthy layer'	240	1087.0	1.1	97.9	0.9	1.10	0.90	0.35	0.99	Slightly gravelly sand, moderately poorly sorted, mesokurtic
Tr. 6, stratigraphic position uncertain	?	458.0	13.1	80.1	6.7	1.09	1.69	0.23	1.18	Gravely sand, moderately sorted, mesokurtic
Tr. 6, stratigraphic position uncertain	?	1197.0	4.3	95.4	0.2	0.99	0.99	0.27	0.94	Slightly gravelly sand, moderately poorly sorted, mesokurtic
Tr. 6 cave pearl and bone layer	110	487.0	53.3	45.9	0.6	-0.84	2.14	0.24	0.78	Sandy gravel, very poorly sorted, platykurtic
Tr. 6, Hearth 1	120	390.0	6.1	91.0	2.8	1.13	2.27	0.18	1.33	Gravely sand, poorly sorted, leptokurtic
Tr. 6, 'brownish earthy layer'	150	1615.0	0.8	98.7	0.3	1.12	0.90	0.32	0.86	Slightly gravelly sand, moderately poorly sorted, platykurtic
Tr. 6, 'brownish earthy layer'	200	2225.0	1.9	94.9	3.1	1.06	0.91	0.20	1.25	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. 6, 'brownish earthy layer'	250	1427.0	9.6	89.8	0.5	0.95	1.49	0.15	1.69	Gravely sand, poorly sorted, leptokurtic
Tr. 8? Hearth 2?	?	1423.0	17.2	82.6	0.0	0.34	1.44	-0.41	1.45	Gravely sand, poorly sorted, very leptokurtic
Tr. A1, Grey 'Ashy' lens	105	501.0	26.0	73.7	0.1	0.38	1.65	0.30	0.66	Gravely sand, poorly sorted, platykurtic
Tr. A 1, 'rubbly layer'	110	221.2	39.9	57.7	2.3	0.15	1.67	-0.12	0.68	Sandy gravel, poorly sorted, platykurtic
Tr. A 1, 'earthy layer'	130	1216.0	3.3	94.7	1.8	1.03	0.94	0.21	1.14	Slightly gravelly sand, moderately sorted, leptokurtic
Tr. A 1, 'rubbly layer'	152	1396.0	2.7	94.5	2.6	1.18	1.07	0.15	1.18	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. A 1 'earthy layer'	170	1245.6	8.1	89.7	2.1	1.10	1.29	0.10	1.63	Gravely sand, poorly sorted, leptokurtic
Tr. A 1, 'rubbly layer'	230	1504.2	19.8	79.6	0.5	0.21	1.58	0.01	1.07	Gravely sand, poorly sorted, mesokurtic
Tr. A 1, 'thin flowstone'	234	707.3	1.6	94.0	4.2	1.12	1.16	0.27	1.40	Slightly gravelly sand, poorly sorted, leptokurtic
Tr. A 1, 'earthy layer'	235	252.3	17.5	79.1	3.2	0.57	1.77	0.09	1.43	Gravely sand, moderately poorly sorted, leptokurtic
Tr. A 1, 'dark earthy layer'	250	1178.7	4.7	94.5	0.7	1.02	1.08	0.09	1.39	Slightly gravelly sand, moderately poorly sorted, leptokurtic
Tr. A 1, 'light sandy layer'	264	2797.4	15.8	76.0	8.1	1.44	2.03	0.14	1.03	Gravely sand, moderately sorted, mesokurtic
Tr. A 1, 'earthy layer with thin sheets of flowstone'	280	851.4	4.8	84.3	0.8	0.78	1.54	0.26	0.87	Gravely sand, poorly sorted, platykurtic
Tr. A 1, 'banded earthy layer'	288	1610.6	1.3	97.3	1.2	0.90	0.80	0.39	1.60	Slightly gravelly sand, moderately sorted, very leptokurtic
Tr. A 1, 'banded earthy layer'	300	1023.4	3.7	94.1	2.1	1.14	1.06	1.25	1.13	Slightly gravelly sand, poorly sorted, leptokurtic
Tr. A 1, stratigraphic position uncertain	?	1465.6	19.3	79.1	1.4	0.17	1.53	0.03	1.40	Gravely sand, poorly sorted, leptokurtic

samples contained more than 90% and 26 samples more than 75% sand, but only 1 sample had more than 50% gravel. Some particle size distribution curves (Fig. 3) illustrate the unimodal nature of the sediments, the bulk of which consist of particles of grain sizes 0.5-1.5 ϕ (coarse/medium sand). The Inclusive Graphic Statistics of Folk and Ward (1957) were calculated for each sample using the computer program SIEVETTE (Shackley 1975) and are also listed in Table 1. They show the mean grain size of the sediments to be 1.17 ϕ (medium sand), and that the skewness values tend on the whole to be positive. However, the existence of 4 samples with negative skewness values is interesting, since this feature has been taken by many workers (for example Friedman 1961) as typical of beach sands.

The most important result of this analysis is to emphasise the striking uniformity of the deposits, which are composed of sand of very similar textural composition. This is an unusual feature of cave deposits which, since they are formed under rather complex sedimentological conditions, tend towards greater variety. It seems unlikely that the results of this analysis can be of any value in detecting definite trends, or in defining stratigraphic horizons. Minor textural differences are principally attributable to variations in the amount of coarser clastic particles weathered from the cave walls, and to later disturbance, and no palaeoenvironmental evidence of value can be deduced from these results. The sediments are mostly consolidated and the baulks of the trenches need no supports. Thin section study combined with treatment by hydrochloric acid showed that this consolidation was due to a calcite cement.

Origin

The cave sediments could either be derived from weathering of the aeolianite inside the cave or from material weathered outside the cave and redeposited. In either case the primary source is the aeolianite but the weathering products have been mixed with organic matter and humus from exterior topsoil, together with the debris of human and animal occupation. The source material controls to a large extent the nature of the weathering products, and in this case the cave sediments directly reflect the composition of the aeolianite.

The cave deposits have been subjected to some degree of diagenesis, including the formation of speleothems and gypsum. Their characteristics therefore depend on the textural and mineralogical characteristics of the lithified dune and beach sands, subsequent weathering, transport, and renewed diagenesis. These features and processes are related to climate, but the nature of the resulting sediments suggests that it was not the controlling factor, a situation quite contrary to that generally found in European caves.

The stages in the formation of the deposit are shown diagrammatically in Fig. 4. The sediments in question bear many relict features

from previous stages in the cycle, for example the negative skewness values of some layers of sediment, which seem likely to be related to the original composition of aeolianite.

At present the primary sedimentological process operating within the cave is the deposition of calcium carbonate as a cementing agent, but very little active weathering occurs. It is therefore difficult to envisage the production of the deposit *in situ* as the exclusive product of weathering under a different climatic regime. It also seems unlikely that local macroclimate greatly influences the microclimate of the cave, certainly not enough to produce this type and depth of deposit.

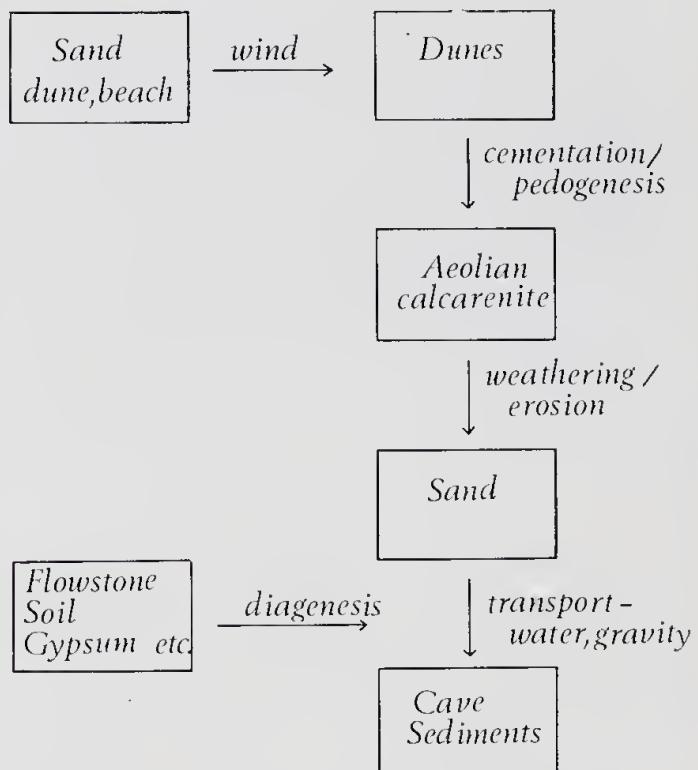


Figure 4.—Flow diagram indicating the processes which have contributed to the formation of the Devil's Lair sediments.

This suggests that the deposits were derived from material weathered from the aeolianite outside the cave, and redeposited inside, via the north entrance. The nature of the material and of the cave entrance suggest that wind was not the transporting medium, and it is suggested that the material either arrived in water-transported 'bursts', as suggested by Dortch and Merrilees (1973) as a result of especially heavy rainfall, or that it arrived as a continuous slow trickle.

If sediment had accumulated on the surface during the dry season and was then washed into the cave during the rainy season, one would expect more systematic laminations and a greater variation in the nature of the sediments. Laminae were, however, more obvious in Trench 9 (nearer the cave wall) than in

Trench 5, at the same stratigraphic levels. However, the lack of more extensive laminae does not necessarily negate the 'burst' sedimentation theory, since there seems to be no sedimentological process which could produce such a very slow rate of accumulation, less than 1 mm per year, if it were continuous.

An examination of the surface textures of the cave sediments shows them to be identical to those of the aeolianite, although showing evidence of many different sedimentological processes, and there seems to be no doubt that this was the source material. The composition of the topmost ('dark earthy') layer is rather different, and it has a high clay and humus content, which suggests that it was primarily derived from topsoil, washed into the cave from the south entrance after the north entrance became sealed by the talus cone.

The very slow rate of accumulation is indeed remarkable, and was commented on by Lundelius (1960) as well as by later workers. Dortch and Merrilees (1972) consider that the rapid burial of a prominent stalagmite indicates a fast rate of deposition for the upper part of the deposit, and they suggest that accumulation of sediment in the cave was not slow, but intermittent. The writer agrees with this.

A series of samples taken from depths of 320, 250 and 200 cm below cave datum in Trench 8₂ which would span the maximum cold of the last glaciation (the period 23 000-16 000 BP) show no appreciable variations. If the variations in the sedimentation pattern of the cave had been attributable to climatic fluctuations then it would be expected that these samples would show considerable differences. Analysis showed them to be similar in colour, phosphate and humus content, as well as in particle size. No variation in grain surface texture could be observed under the microscope and the conclusion was drawn that either there had been no major climatic change or that the cave sedimentation was independent of macroclimate. The period covered by these samples would be included in the major recorded fall in sea level between 40 000-15 000 BP, but it has been suggested that local climate did not change drastically during this period. However, it would seem that climate had little influence over the sedimentation pattern, unless increased rainfall at any period stimulated more sedimentation 'bursts'. This might well have happened in the upper part of the deposits.

A study of the faunal changes in Devil's Lair (Baynes, Merrilees and Porter 1976) suggests the possibility of an alteration in the position of the forest zone near Devil's Lair, perhaps related to a glacioeustatic rise in sea level. It seems probable that some time after 19 000 BP the sea west of the cave fell at least 100 m below its present level, and then began to rise again, reaching a level of -40 m by 12 000 BP and its present level some time during the post-glacial (Baynes, Merrilees and Porter 1976). It is clear then that the deposition of the 'first orange brown earthy layer', bounded by a radiocarbon date of 19 000 BP at the base and 12 000

BP at the top, must have taken place during a period of marked palaeoenvironmental change. Bearing in mind that at some time during this period the sea would have been as much as 20 km further away from the site than at present, and that climate, weathering and erosional processes must inevitably have fluctuated, one can say that the uniformity of the deposits must indicate independence of climatic control.

Flowstone horizons

Composition

Two distinct varieties of speleothems are present in Devil's Lair, discrete stratified flowstone layers occurring approximately parallel to the surface of the floor on which they are formed, and secondary calcitic penetration of the clastic sediments. In addition to these forms, individual stalagmites occur, such as the one figured by Dortch and Merrilees (1972). Many of the flowstone layers in the cave are rather thin, of the order of 1 cm in thickness. The flowstone levels seem often to be associated with quantities of charcoal, sometimes included within them and sometimes occurring as charcoal rich bands immediately underneath. Although the flowstones consist mainly of calcite precipitate they may also contain quantities of clastic deposits, but there are sharp boundaries with the overlying clastic layers; they are composed of large (> 0.02 mm) clear, elongated crystals whose long axes occur perpendicular to the precipitating surface.

Formation

Calcitic flowstones are formed by the precipitation of calcite from thin films of water. However, only a small quantity of water is required and this can be met with under a variety of climatic conditions. There is no close relationship between flowstone formation and climatic control, although it is a common assumption that the deposition of flowstone layers represents a wet episode should a large quantity of water be required. Two main factors seem to control the formation of flowstone layers, the most important being the rate and continuity of clastic sedimentation, and secondly, and to a lesser extent, fluctuations in surface climate which produce changes in vegetation and thus changes in the amount of carbon dioxide which is dissolved in the groundwater.

Frank (1973) noted that the rates of clastic alluviation in caves, particularly in entrance facies, far exceed the precipitation rate of calcite, and may even be deposited 7 times as fast as stalagmite could possibly accumulate. This is important for Devil's Lair, where it is suggested that the majority of the clastic material entered the cave very fast indeed, as 'bursts', which were intermittent and resulted in an overall slow rate of sedimentation. Thus it would clearly have been impossible for flowstones to have developed during a sedimentation 'burst', irrespective of the amount of ground water available.

Kukla and Lozek (1958), working on similar problems, concluded that the presence of flowstones in a clastic sequence indicated a slowing down or a complete cessation of clastic deposition. It is therefore clear that whatever the climatic fluctuations the flowstone layers within the cave mark periods of pauses in sedimentation, and must also mark periods when the cave was not being utilised either by animal or human groups, since this would have necessitated an open entrance which would have permitted sediment accretion. It is unlikely that extensive deposits of flowstone could have formed while the entrance was open. This does not preclude the inclusion of biotic or archaeological remains within the flowstone, since as flowstone deposition was rather slow it is inevitable that even the action of gravity would result in some debris becoming incorporated into the layers, or flowstone would accumulate round objects protruding from the general surface.

Butzer (1971) stated that a sub-humid moisture regime and a temperate climate is optimum for speleothem formation. Corbel (1952, 1959, 1961) estimated that when the mean annual temperature is greater than 18°C and the mean annual rainfall exceeds 1 000 mm speleothems would form in all parts of a cave. The present climate around Devil's Lair is far milder than these limits, but the cave interior is still rather damp, with calcareous solutions dripping inside the cave during the wetter months. Speleothem formation is still continuing at the present day, although not resulting in continuous flowstone layers.

It is possible (Baynes, Merrilees and Porter, 1976) that both temperature and quantity of rainfall may have increased between 19 000 and 12 000 BP, and that this may have had some effect on the deposition of the upper flowstones. However, the solution and precipitation of calcite is not only dependent on temperature and rainfall, but is also a function of the availability of carbon dioxide, so that the control is indirect since it is the surface vegetation and soil micro-organisms which control carbon dioxide availability. Schmid (1958, 1963) and Kukla (1961) maintain that speleothem growth is enhanced by warm humid climates where there are substantial amounts of surface vegetation to provide the carbon dioxide for the solution of calcite, and then enable calcite-laden water to precipitate the mineral after entering the cave.

Frank (1973), in a study of flowstone layers in Australian caves, stresses the relationship between cessation of clastic deposition and the formation of flowstone, and the fact that the latter is not climate-dependent. It seems reasonable to regard the flowstone layers in Devil's Lair as marking sedimentation pauses, probably resulting from the temporary blocking of the cave entrances, rather than as intervals of warmer, wetter climatic conditions. However, bearing in mind the conclusions of Gams (1968), working on the Postojna cave, which provided additional support for the theory that a surface environment of high precipitation and

dense vegetation is optimum for encouraging speleothems, it is worth considering in the case of Devil's Lair that an increase in local vegetation cover might be a contributory factor in flowstone formation, especially in the thick flowstone at the top of the deposit. This layer, visible for example at the top of the west face of Trench 5 (Dortch and Merrilees 1973, Fig. 5) was clearly deposited after 12 000 BP, before the deposition of the 'dark earthy' layer, 325 ± 85 BP, which originated through a different set of processes and via a different cave entrance. It seems likely that the processes responsible for the deposition of the main bulk of the clastic sediments became inoperative around 12 000 BP and that the sedimentation pattern of the cave was interrupted. After this time the thick band of flowstone was deposited and sedimentation then resumed, resulting in the 'dark earthy' layer which has a high humus content and seems largely to consist of redeposited topsoil. The depositional hiatus marked by this thick and very complex multiple flowstone was almost certainly caused by the blocking of the north entrance.

Diagenesis

The clastic cave sediments are characterised by their mostly inherited features which reflect previous depositional environments. Transport into the cave has had little influence on the sediments, but diagenesis, which to some extent reflects climate, has left some imprint. Diagenetic processes include lithification through carbonate cementation, the formation of gypsum deposits, movement of soil phosphates, humus and soluble salts, in addition to biogenic disturbance through, for instance, penetration of rootlets and human activity.

Human and animal activity

Human activity is evidenced principally by the disturbance of the deposits, for example by digging of pits and the remains of hearths, and by the addition of archaeological material, either artifacts or food debris.

Human groups entering the cave have also resulted in the addition of phosphates together with increments of humus and plant material from outside. Animal activity has proceeded along similar lines, again resulting in disturbance and also in waste breakdown products such as collophane.

Several lenses have been recognised as hearths on the basis of increased charcoal content and the presence of burnt bone. Examination of such hearth deposits under the microscope showed that the quartz sand grains were heavily coated with smaller particles, giving them a 'dusty' appearance, and that many agglomerations of cracked and burnt grains occurred. Modifications of grain surface texture included mazes of fine cracks, angular splitting and encrustations of charcoal. These microscopic characteristics reinforce the interpretation of hearths.

Lithification

The process of lithification of the sediments by the addition of calcitic cement is certainly the most important diagenetic process operating. This must be carefully distinguished from the formation of flowstone, since the calcite precipitation here occurs after the deposition of the clastics, the grains are smaller, crystal formations unclear and there are no defined boundaries between calcite cement and clastic grain. The cohesion imparted by this process has already been discussed. All the Devil's Lair deposits have been affected to some degree, and in some cases this has resulted in lithification. The chemical processes are, however, similar to those active in the formation of flowstone, namely the precipitation of calcite from solutions rich in carbon dioxide, but this occurs after the deposition of the clastics and is a continuing process.

Formation of gypsum

Minor deposits of gypsum are found within the deposits, frequently associated with rootlets and occurring in larger concentrations around roots and root holes. The finest rootlets are often completely coated in white gypsum, and occasionally moulds are left where roots have once been. Under normal weathering any sulphide present in bedrock is oxidised to sulphate, and in the course of soil formation the sulphate becomes available to plants and micro-organisms, and part of it is leached. Under temperate conditions and in well drained soils, the sulphur is present in organic matter, probably in amino acids such as cystine and cysteine, but most is removed by leaching. Under more arid conditions it is retained and often separates out as gypsum deposits. Oxidation of sulphides present in organic matter and plants is catalysed by the action of bacteria which make use of the energy released. Leaching is not an important process within these cave sediments. The gypsum deposits appear to have formed around the roots by the processes described above, and the movement of water within the cave sediment is not sufficient to disperse them.

Conclusions

In any study of this type it is important to relate the deposits to the morphology and bedrock of the cave, and in this case the latter is of paramount importance. The aeolianite in which the cave is developed has governed the formation and constituents of the sediments, and any other factors including climatic variations, human or animal activity, being of only secondary importance. The sequence of deposits is interesting because of extreme textural uniformity, seemingly independent of macroclimatic influences. The primary source of the cave sediments is undoubtedly weathering of the aeolianite, additional material being washed and blown in from outside, or brought in by animals or human groups visiting the cave. Flowstone formations, which constitute a substantial part of the sequence and are interleaved with the clastic sediments, are related to pauses in clastic sedimentation caused by blocking of the cave

entrances. The cohesion of the deposits is effected by secondary accretion of calcium carbonate around the quartz sand grains, forming a cement. The deposits retain many of the features of previous stages in the depositional cycle, a situation completely contrary to that found in any of the limestone caves of the northern hemisphere. It is suggested that the sediments accumulated in intermittent bursts, perhaps related to episodes of increased rainfall.

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The Dunsborough implement: an Aboriginal biface from southwestern Australia

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Abstract

A chert artifact superficially resembling a Palaeolithic biface has been found at Dunsborough, Western Australia. It is distinctively coloured, but otherwise resembles petrographically the Aboriginal artifacts of Eocene bryozoan chert previously described from southwestern Australia. The presence of *Nothofagidites* sp. and *Haloragacidites harrisii* (Couper) Harris, rules out European origin. Other microfossils indicate Early or Middle Eocene age for the chert. The Dunsborough implement, and another biface from a nearby site, are made of rock probably quarried west of the present Western Australian coast in the late Pleistocene or early Holocene, when sea level was lower. The investigation emphasizes the potential value of palynological examination of chert implements particularly when exotic origin is suspected.

Introduction

Over the past half century, numerous large bifacially flaked stone implements have been found in Australia, particularly at sites in the coastal districts of southeastern South Australia and western Victoria (Fig. 1). Most are of Aboriginal origin, but several are European, the best known being Palaeolithic implements picked out of English flint ballast dumped by sailing ships at Port Lincoln, South Australia (Fig. 1). The latter implements are displayed at the South Australian Museum.

The most controversial of these bifacially flaked pieces is the Scaddan implement (Fig. 2), a flint biface closely resembling an Acheulian hand axe, which was collected at Scaddan near the south coast of Western Australia (Fig. 1). The specimen was early recognised as problematical (Noone 1943), though Tindale regarded it as an Aboriginal artifact (Tindale 1941, p. 145; 1949, p. 165). A decade later McCarthy stated that the Scaddan implement resembled "more closely the flint *coup-de-poing* from Europe, examples of which, brought here by various people or in ships' ballast, have found their way into strange places in Australia." (McCarthy 1958, p. 178).

In 1976 two of us (CED, JEG) carried out an archaeological and petrological study of the Scaddan implement (Dortch & Glover in press) and concluded from its technology and style, its stone texture, surface patination and colour, and its rolled condition, that it is much more likely to be of English than Australian origin. Unfortunately the contained microfossils were poorly preserved, and gave no conclusive information about the origin and age of the stone.

Soon after the analysis of the Scaddan implement, another large flint or chert biface somewhat resembling a Palaeolithic hand axe was found by a schoolboy, Clayton Wholley, at the small coastal resort of Dunsborough some 200 km south of Perth (Fig. 1). The implement was in a vacant block of land from which the vegetation had been partly cleared in preparation for building. When first seen it was partly exposed in the surface of a sandy deposit which has been extensively disturbed during the European era.

Now, artifacts of Middle or Late Eocene chert are of particular interest in the prehistory of the Perth Basin and adjacent areas. They characterize late Pleistocene and early Holocene assemblages, but their source has never been found because it was probably submerged about 6000 BP (Glover 1975). Consequently the presence or absence of these artifacts in an assemblage provides archaeologists with a pointer to its age.

There are therefore several reasons for reporting on the Dunsborough implement in detail, and establishing the age of the chert. This paper gives an archaeological description of the Dunsborough implement, describes its petrology and palynology, and discusses its history and its relationship to other Western Australian chert artifacts. In particular, the investigation shows how palynological techniques may illuminate the origin of chert implements, and how they can distinguish transported Acheulian hand axes from Australian implements of similar appearance. The responsibilities of the authors are as follows: archaeology, CED; petrology, JEG; palynology, BEB.

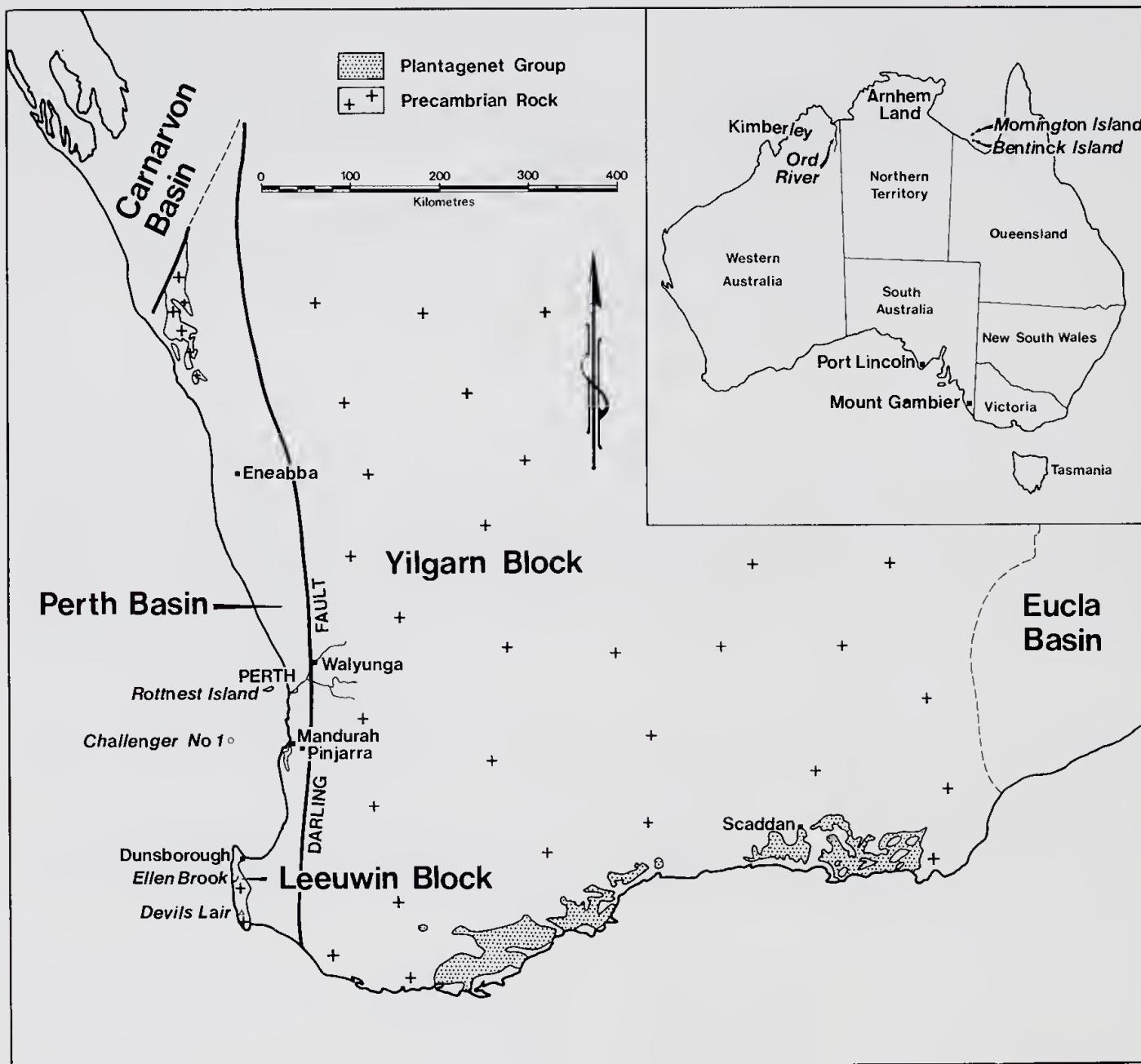


Figure 1.—Map showing localities mentioned in the text.

Archaeological description

The Dunsborough implement (Fig. 3) is a complete, invasively flaked chert biface. It weighs approximately 300 g and has the following dimensions: length 106 mm; width 83 mm; and thickness 46 mm. In plan view or outline the piece is sub-oval, and it is roughly elliptical in section. About one third of one face (Fig. 3, right) retains a cortex surface. A single positive conchoidal fracture extends over much of the opposing face (Fig. 3, left) and so the implement is probably made on a single large flake. The right-hand and lower edges of the piece (Fig. 3, right) are broad and thick with deeply biting, bold flake scars, whereas the left-hand and upper left edges shown in the same figure have much more

acutely angled edges produced by shallower and more invasive bifacial flaking. (The latter angles are not apparent in the side view shown in Fig. 3, centre.)

The piece shows very clear abrading and crushing, i.e. multiple, overlapping and very small (0.5-5 mm) conchoidal fractures, on parts of its lateral edges and particularly on the low ridge running down the lower centre of the face shown in Figure 3, right. The crushing on this ridge encroaches over the adjacent flake scar ridges and facets, clearly post-dating them. Most of the other flake scar ridges on both faces are undamaged or only very slightly so. The two fan-shaped scars extending left of the abraded ridge in Figure 3 right, and also several much smaller scars immediately

to the right of the ridge, seem to originate from a single source of percussion. Possibly then this face was used as an anvil or hammer surface; on the other hand these scars could be the result of glancing percussion occurring when the piece lay with its face exposed to stones carried in high-velocity water flow. The proximity of these flake scars to the abraded central ridge, the virtual absence of abrading or battering on the opposite face of the piece (Fig. 3, left), and its differentially abraded lateral edges, all suggest that they are the result of use, or perhaps a combination of use and some natural abrasion.

The fragmentary remains of the calcareous shell of a marine invertebrate adhere to one face (Fig. 3, right, lower right corner). As the shell is of recent origin the implement must have been submerged only a short time before being found and so the piece was not in primary position when collected.

Stylistically the Dunsborough implement does not closely resemble any of the classic forms of Acheulian or Mousterian hand axes from north-western Europe (cf. Bordes 1961; Roe 1968; Wymer 1968). However its surface colouration and texture, size, and general morphology place it within the range of biface variation known from European Palaeolithic assemblages.

Petrology

The surface colour of the implement ranges from medium bluish grey (5B5/1) to greenish grey (5GY6/1) and yellowish grey (5Y7/2) (See Rock-color Chart Committee 1963 for comparative colours, and explanation of the symbols). A section through the implement shows that it is rimmed locally by a bluish white (5B9/1) patina up to 2 mm thick. Inward from the patina, the core ranges from medium grey (N5) to very light grey (N8), and there is a small, light brown (5YR6/4) area about 1 cm long stained by iron oxide.

The rock is a fossiliferous chert with abundant silicified Bryozoa and Foraminifera, in a matrix of cryptocrystalline silica (average grain size <0.01 mm in diameter). There are numerous patches of coarser chalcedonic quartz (average grain diameter 0.03 mm), and some tests have an infilling of coarse, drusy chalcedony with a core of granular quartz. Siliceous spicules are also present, but their original composition is uncertain.

A feature of many of the silicified tests is a very fine fringe, generally directed inward from the test wall. The fringe is formed of colourless, roughly wedge-shaped bodies, commonly about 0.01 mm long, with a pronounced nega-

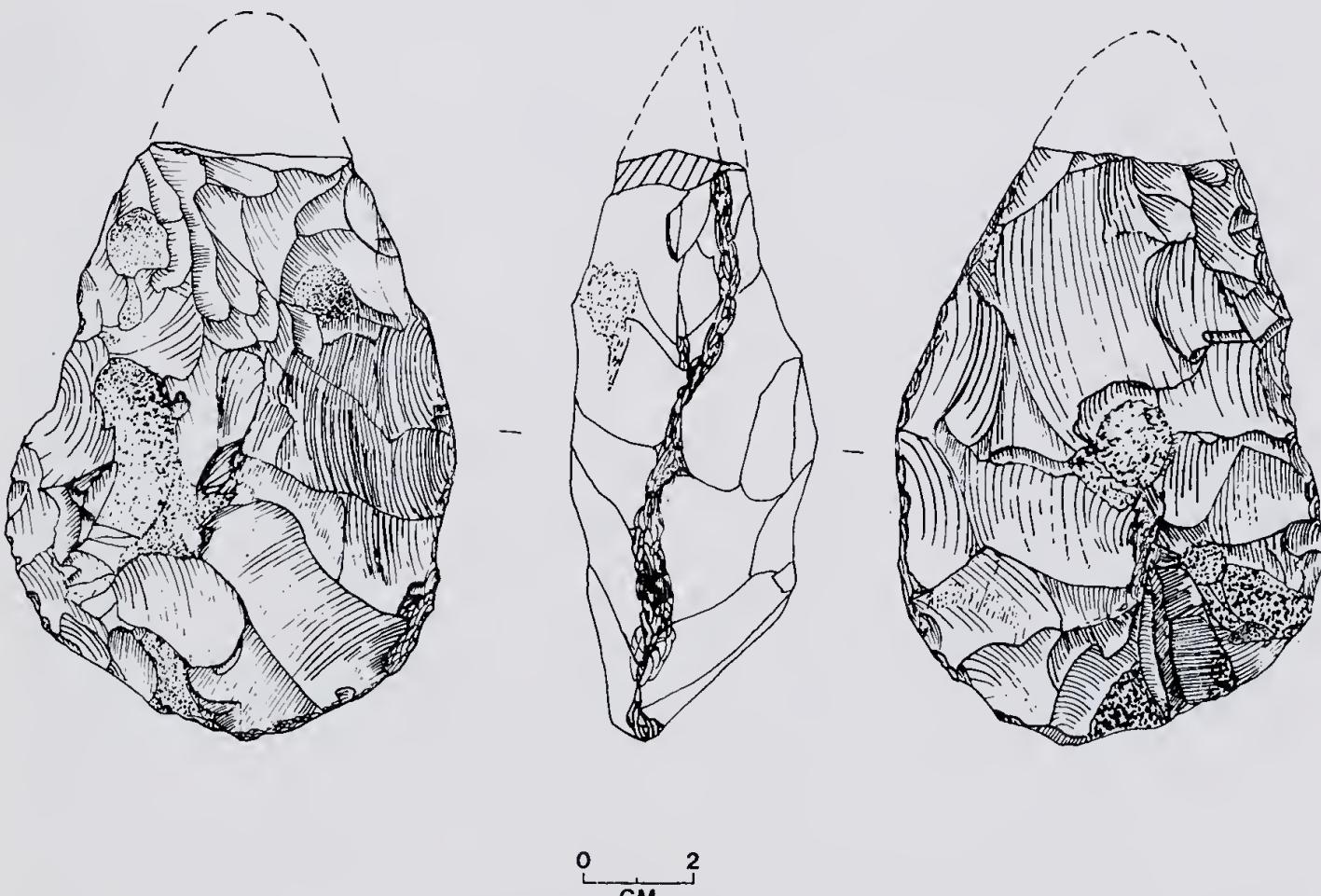


Figure 2.—The Scaddan implement.

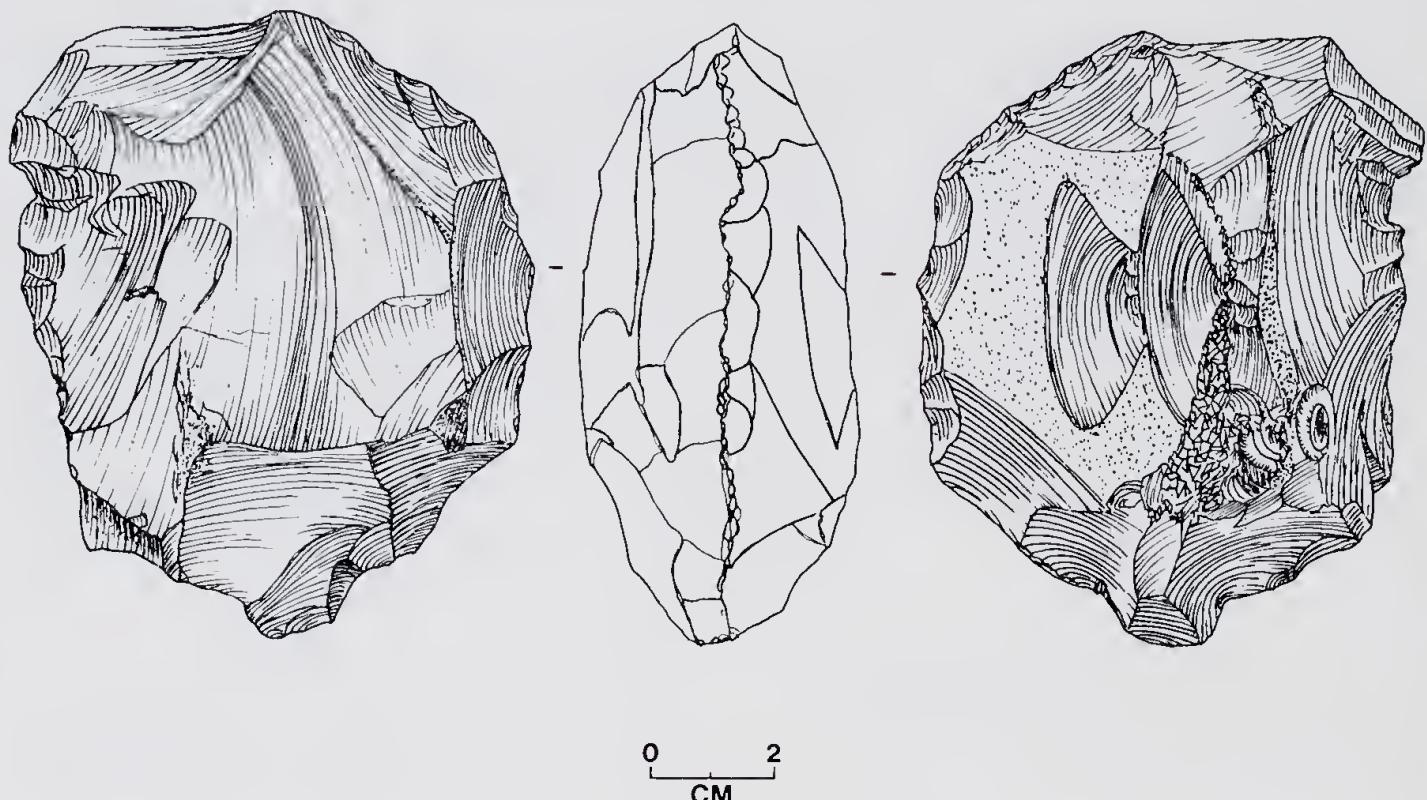


Figure 3.—The Dunsborough implement.

tive relief that causes them to appear dark under low magnification. The bodies were first thought to be opal, but their negative relief is too strong. Their drusy habit suggests that they are cavities left after solution of drusy calcite that was not replaced by silica. Whatever their origin, these features are common in Western Australian Eocene chert.

Other material in the chert includes rare glauconite pellets, silt-sized clastic quartz, grey, finely disseminated clay, and fragments of plant microfossils.

Comparison with chert flakes

The Dunsborough implement was found in an area from which flakes of chert, quartzite, mylonitic rock and silcrete were recovered. Quartzite is quite abundant. A broken pebble of granitic rock was also collected.

Chert flakes are common in the Perth Basin, particularly in the western part of a belt extending between Eneabba and Mandurah (Glover 1975). Many of these flakes contain Eocene Bryozoa, and the Middle and Late Eocene foraminifer *Maslinella chapmani* Glaessner and Wade has been identified in two of them (Glover & Cockbain 1971). More recently, concentrations of similar flakes have been found in blow-outs in sand on the western part of the Leeuwin Block. Petrologically, there is nothing to distinguish the chert flakes found at Dunsborough, or elsewhere in the Perth Basin or Leeuwin Block, from the chert of the implement. There is, however, a difference in surface colour. Most of the flakes in the Perth

Basin range from white, through shades of grey, brown and orange, whereas the implement has blue and green tints noted elsewhere only in two of the Dunsborough flakes. The significance of these colours is uncertain, because the colour of many flakes seems to be at least partly influenced by the colouration of the sand in which they are found.

Palynology Treatment

Inorganic and oxidisable organic materials were removed by boiling about 2 g of the crushed chert in HF, followed by warming the residue in 10% HCl and oxidising the acid-insoluble fraction with concentrated HNO₃. A small quantity of microscopic plant fragments remained. Because the number of identifiable plant microfossils in the final residue was small, three separate preparations were carried out to guard against misinterpretations resulting from laboratory contamination.

Plant microfossils

Plant microfossils were recovered from each of the three preparations. Small cuticular pieces and woody tissues predominated, but fragmental dinoflagellates of the *Spiniferites*-type were fairly common. No more than about 10 identifiable microfossils were found in each of the residues. However, the assemblages were consistent and the same forms were recognised in all three. It was therefore concluded that the plant microfossils were derived entirely from the material of the biface. All the species identified are listed below:

Spores and pollen:

Cyathidites sp.
Haloragacidites harrisii (Couper) Harris
Nothofagidites sp. (*Nothofagus brassii*-Group)
 Microplankton:
Leiosphaeridia sp.
Veryhachium sp.
Homotryblium floripes (Deflandre & Cookson)
 Stover
Spiniferites sp.
Dejlandrea sp. (hypotract only)
Rcttnestia borussica (Eisenack) Cookson & Eisenack
Wetzelia sp. cf. *W. lineidentata* Cookson & Eisenack
Leptodinium maculatum Cookson & Eisenack.
?Schematophora sp.
Baltisphaeridium paucifurcatum (Cookson & Eisenack) Downie & Sarjeant
 Reworked microfossils:
Microbaculispora tentula Tiwari (Permian)
Plicatipollenites sp. (Lower Permian)
Cycadopites cymbatus (Balme & Hennelly)
 Segroves (Lower Permian)

The presence of *Nothofagidites* sp. and *Haloragacidites harrisii* rule out any possibility that the chert is European. Both these species are typically southern hemisphere forms that range from the Late Cretaceous to the present. In Western Australia they are frequently associated in Eocene assemblages and in this State *Nothofagidites* has not yet been recorded from sediments older than Eocene.

Wetzelia is unknown from pre-Tertiary strata. Its first appearance is in the Early Palaeocene of North America and its latest occurrence in the Middle Miocene of Europe (Harker & Sarjeant 1975). In Australia it particularly characterises Eocene sediments. Stover (1975) discussed the stratigraphic distribution of *Homotryblium floripes* which was recorded by Cookson and Eisenack (1961) from the Kings Park Formation, between 451 and 486 m in the Rottnest Island bore. Current opinion regards this section of the Kings Park Formation as Early Eocene (Cockbain & Ingram quoted by Quilty 1974). According to Stover, the species ranges into the Early Miocene. The type material of *Leptodinium maculatum* Cookson & Eisenack also came from the interval 453-486 m in the Rottnest Island bore. This is the only published record from Australia, although a similar form occurs in the Lower and Middle Eocene of Europe.

The other dinoflagellates present are all consistent with an Early Tertiary age, although they are less important, either because they are long-ranging forms, or because the identifications are uncertain.

Considering the sum of evidence, the most likely age of the assemblage is Early or Middle Eocene. Comparisons with published data from Australia further strengthen this conclusion. In particular, there are striking similarities between the microfossil assemblage from the biface and those recovered from sediments in the interval 453-485 m in the Rottnest Island bore (Cookson & Eisenack 1961; Hassell & Kneebone 1960). All the plant microfossils listed, or closely similar forms, have been previously recorded from samples in this interval,

with the exception of reworked Permian microfossils. As an additional check, material from the Rottnest Island bore, prepared by Dr C. W. Hassell and retained in the collections of the Department of Geology, University of Western Australia, was re-examined. Rare Permian saccate pollen grains and a specimen of *Microbaculispora tentula* Tiwari were found in a smear mount prepared from a core cut in the interval 451-470 m. The source of these reworked Permian pollen grains is obscure. No exposures or shallow subsurface occurrence of Permian strata are known in the vicinity of Rottnest Island. As reworked Cretaceous pollen are also present in the Tertiary assemblages, it is possible that the Permian forms represent second-cycle reworking, from Mesozoic sediments.

In summary, the palynological evidence points irresistibly to the conclusion that the biface is made of Early or Middle Eocene chert, obtained either from the Kings Park Formation or a unit correlating with it.

Stratigraphic source of the chert

The source of the Dunsborough implement, and of petrographically similar chert pieces, is bound up with the distribution of Eocene rocks in the southwest of Western Australia. There is only one sequence of Eocene rocks cropping out in the region, namely the Late Eocene Plantagenet Group, which is distributed within an irregular belt along the south coast, and is a local source of chert for artifacts. Colloform opal is common in chert flakes from the Plantagenet Group, but is absent from flakes on the Leeuwin Block, and in the central and northern Perth Basin.

The only unit described from the Perth Basin that contains Eocene rocks is the sub-surface, Palaeocene-Early Eocene Kings Park Formation (Quilty 1974). However, palynological evidence suggests that the interval from this formation intersected between 451 and 486 m in the Rottnest Island bore extends to the Middle Eocene. In addition, Quilty (pers. comm. 1975) has recognized unnamed Late Eocene strata, including chert, from the interval between 510 and 590 m in WAPET's Challenger No. 1 well, about 60 km west of Mandurah. There are clearly gaps in our understanding of the Eocene stratigraphy of the Perth Basin, and published information is far from comprehensive.

The chert of flakes from the Perth Basin has been dated as Middle or Late Eocene from Bryozoa and Foraminifera. It has been argued that the concentrations of Perth Basin chert flakes in the Eneabba-Mandurah belt, and their increase in frequency westward, point to derivation from westward sources that were submerged as the sea rose to its present level (Glover 1975). More recently, indendent radiocarbon evidence from excavations at Walyunga shows that the source of chert for artifacts was eliminated between 6135 ± 160 and 3220 ± 100 years ago (Pearce, pers. comm. 1976). Recent work has also revealed additional con-

centrations of chert flakes near the western margin of the Leeuwin Block, and it can be argued that those also come from the west.

The flora of the Dunsborough implement correlates well with that of the Early or Middle Eocene rocks in the interval of Kings Park Formation between 451 and 486 m in the Rottnest Island bore. As these rocks do not crop out, the source of the implement is best sought seaward. Rocks of the Kings Park Formation would have been exposed in the valley of the ancestral Swan, and probably elsewhere in windows through the veneer of later rocks. The Kings Park Formation lenses out around the latitude of Pinjarra, and off-shore rocks of equivalent age in the Dunsborough region may have yielded the implement.

Unfortunately, the chert flakes assumed from the Bryozoa and Foraminifera to be Middle or Late Eocene, have not yielded palynological residues sufficiently well preserved to compare with the residues from the Dunsborough implement. The various flakes and the Dunsborough implement may therefore have come from rocks of the same age, or of somewhat different age and stratigraphic position within the Eocene Series.

Discussion

The best documented concentration of large, invasively flaked flint bifaces on the Australian continent is in the assemblages noted earlier from sites in southeastern South Australia and western Victoria. Tindale (1941) designated these assemblages as the "Gambieran" industry, because there is a concentration of them near Mt Gambier, South Australia. Illustrations of selected specimens of flint bifaces from this district (Mitchell 1949, Figs. 32, 33; Stapleton 1945, Figs. 1, 10, 11) clearly show them to be remarkably similar to Old World Palaeolithic hand axes, a fact noted by the two foregoing and other authors (McCarthy 1940, p. 30-33; Mulvaney 1961, p. 71-72; Tindale 1941, p. 145, 165.).

The regional stone industries of Kimberley and Arnhem Land also contain a series of bifacially flaked points and axes in which there are a few pieces resembling Lower or Middle Palaeolithic bifaces. Dortch & Glover (in press) illustrate an ethnographic example of one of these from the Ord valley in east Kimberley. Other large bifaces were collected by the late E. J. Brandl in Arnhem land.

The large picks or "oyster stones" from Bentinck and Mornington Islands, Queensland (Fig. 1), which Tindale (1949, p. 161) describes as being "of crude biface form", in some cases at least are square or rounded in section (Tindale 1949, Figs 6, 11) and so are not truly bifacial. We agree with McCarthy (1958, p. 178-9) that these pieces do not resemble the developed "hand axe" or *coup-de-poing* of the Old World Palaeolithic. Instead they seem to be similar to the more crudely flaked specimens of the *biface abbevillien* and the *pic* of the Lower Palaeolithic of France (cf. Bordes 1961, Plates 88, 90, 91).

Large bifaces, generally of edge-ground form, are known from sites in many parts of Australia (McCarthy, Bramell & Noone 1946, p. 15, 49), including the southwest (Akerman 1973; Ride 1958). However, apart from the "Gambieran" concentration and the few specimens from Kimberley and Arnhem Land, there do not seem to be any other clear regional series of large bifaces resembling those of the Old World Palaeolithic.

Nevertheless the Dunsborough implement is not the only unequivocally indigenous, large biface from the southwest. In October 1976 one of us (CED) recovered a broken chert biface from a coastal blow-out at Ellen Brook 34 km south of Dunsborough (Fig. 1). Numerous chert and quartz artifacts were exposed in the blow-out, and typological and petrological aspects of the assemblage suggest that it is attributable to the early phase of industries identified in the southwest (Dortch 1977; Glover 1975; Hallam 1972).

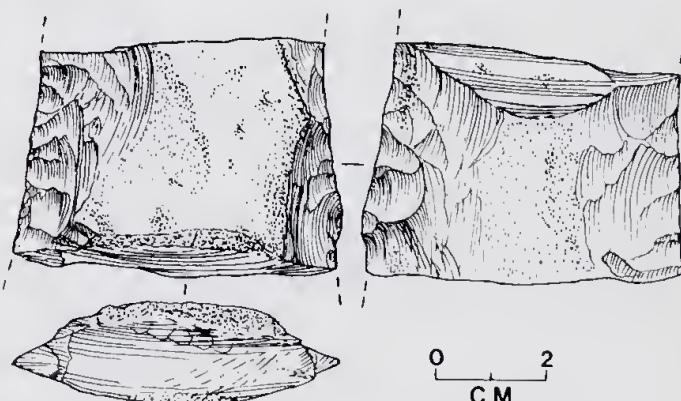


Figure 4.—The Ellen Brook biface.

The Ellen Brook biface (Fig. 4) is an invasively flaked fragment of tabular chert in which both extremities are broken off, perhaps deliberately. The piece is neatly elliptical in section, and both lateral edges are delicately flaked. The specimen is made of the distinctive Eocene bryozoan chert which as noted earlier, characterized southwestern late Pleistocene and early Holocene assemblages.

Part of the significance of the Ellen Brook biface is that, unlike the Dunsborough implement, it clearly shows that southwestern Aborigines were capable of careful, controlled invasive flaking resembling that produced by the "soft-hammer" technique (Bordes 1961, p. 8). Together the Ellen Brook and Dunsborough bifaces confirm Tindale's view that large bifaces are indigenous to the southwest (Tindale 1949, p. 165). However, Tindale based his opinion on the single find of the Scaddan implement (Fig. 2), a specimen which we believe to be probably English in origin. At the same time the view that the Scaddan implement is a "typological and technological anomaly" in southwestern Australia (Dortch and Glover in press) must be amended. Thus, pieces similar to the Scaddan implement were made by

southwestern Aborigines, if only rarely. The probable early Holocene or late Pleistocene ages and early-phase associations of both the Dunsborough and Ellen Brook implements suggest that other specimens resembling Old World Palaeolithic bifaces are likely to be identified in early-phase assemblages in the southwest.

This discussion should end with a note on techniques. Petrology has long been used with some success to trace the history of European and Australian artifacts, but it is not always easy to distinguish between cherts by petrology. Invertebrate fossils can be useful. Floral remains, despite their toughness, do not always survive silicification, as in the Scaddan implement. On the other hand, floral residues from the Dunsborough implement have unequivocally shown its Australian origin. Palynological examination should therefore be attempted whenever an exotic origin is suspected.

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New species of fossil nonmarine molluses from Western Australia and evidence of late Quaternary climatic change in the Shark Bay district

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Abstract

The new species *Coxiella roeae* sp. nov. (Prosobranchia: Hydrobiidae), *Bothriembryon gardneri* sp. nov., *B. consors* sp. nov., *B. douglasi* sp. nov. and *B. ridei* sp. nov. (Stylommatophora: Bulimulidae) are described and figured. All occurrences are believed to be of Pleistocene age.

Coxiella roeae sp. nov. was obtained from lacustrine deposits in the Beermullah district and represents the first fossil species to be recorded for the genus.

The four new species of *Bothriembryon* snails come from fossil soils in the Point d'Entrecasteaux and Shark Bay districts. Those from the former locality, *B. gardneri* sp. nov. and *B. consors* sp. nov., are related ancestrally to living species. The two Shark Bay species, *B. douglasi* sp. nov. and *B. ridei* sp. nov., have no known living descendants. Their extinction, and the apparent subsequent appearance of camaenid snails in the district, are interpreted as evidence of a period of severe regional aridity during the late Pleistocene.

Introduction

This paper describes five new species of molluscs, one freshwater and four terrestrial, from the fossil collections of the Western Australian Museum (WAM) and the Field Museum of Natural History, Chicago (FMNH). The material studied came from three widely separated areas in southwestern Australia (Fig. 1).

Coxiella roeae sp. nov. was obtained in sediments collected from wells, seismic boreholes and other shallow excavations in the Beermullah district, 80 km north of Perth, by Mrs. R. Roe, of "Benalong", Beermullah.

From 1941 to 1976, fossil snail shells have been obtained by a number of collectors from exposures, both natural and man-made, of lithified fossil soils associated with aeolian calcarenite at Point d'Entrecasteaux on the coast of Western Australia south-southeast of the town of Northcliffe. The deposit contains at least eight different species of land snails, of which two, *Bothriembryon gardneri* sp. nov. and *B. consors* sp. nov., are described below.

Collections of land snails from widely dispersed fossil soils in the Shark Bay district, resembling the Depuch Formation, have been found to contain two species of *Bothriembryon* distinct from any now living. These species, which appear to be allopatric, are described as *B. douglasi* sp. nov. and *B. ridei* sp. nov.

A comparison of what is known of modern and fossil land snail distributions in the Shark Bay district suggests that a period of glacioeustatic low sea levels during the late Pleistocene was marked by the extinction of two *Bothriembryon*

species and the subsequent local establishment of up to four species of arid-adapted camaenid snails. These apparent faunal changes are considered to reflect a regional climatic shift towards increased aridity. A relative climatic amelioration appears to have eventuated in the wake of the Flandrian (Holocene) transgression, possibly reflecting the strengthening of maritime influences in the area.

Systematic descriptions

Class Gastropoda
Subclass Prosobranchia
Order Mesogastropoda
Superfamily Rissacea
Family Hydrobiidae

Genus *Coxiella* E. A. Smith, 1894.

Coxiella Smith, 1894. *Proc. malac. Soc. Lond.* 1: 98.
Coxiella Smith; Ludbrook, 1956. *Trans. roy. Soc. S. Aust.* 7: 41 (with synonymy).

Type species (by original designation): *Truncatella striatula* Menke.

From consideration of the shell characters, *Coxiella* has been referred to a diversity of families, e.g., Hydrobiidae subfamily Truncatellinae (Thiele 1931; Macpherson 1957), Coxiliidae (Iredale 1943), Truncatellidae (Cotton 1959; McMichael 1967) and Assimineidae (Ludbrook 1956). Living animals of *C. striatula* have been examined by Dr. G. M. Davis of Philadelphia who states (pers. comm., May 1972) that, in characters of the head-foot morphology, mode of progression, form of the eyes and tentacles and the radula, they show affinity with the Hydrobiidae and not the Truncatellidae; clarification of the subfamily position requires further study.

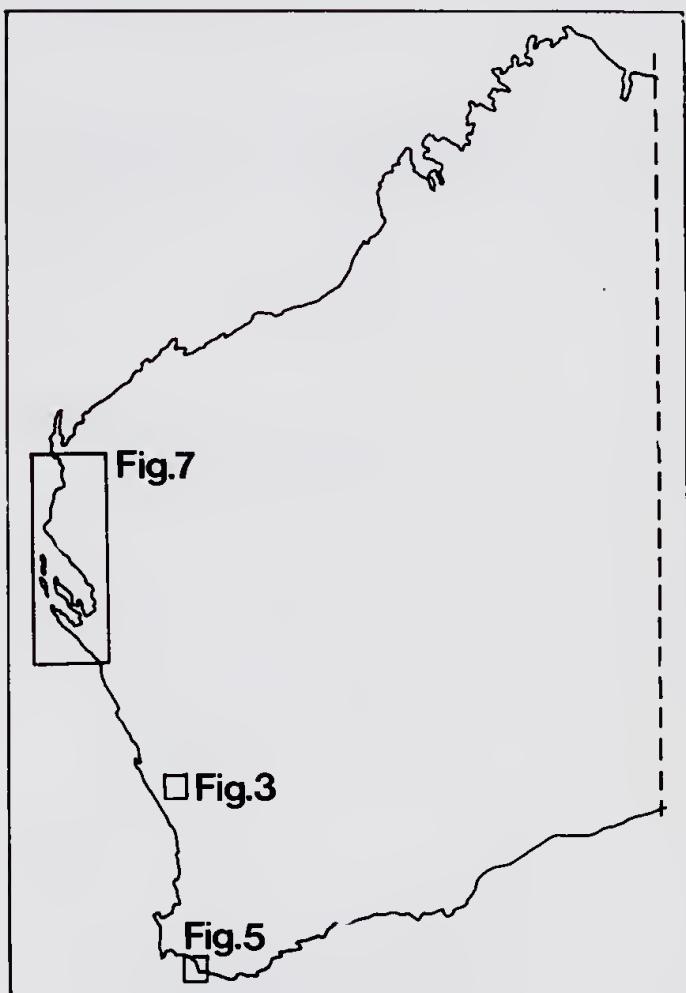


Figure 1.—Western Australia, areas studied.

Coxiella roeae sp. nov.
(Fig. 3)

Material. Holotype WAM 73.4. Paratypes WAM 73.5 (40 shells). Other topotypic reference material WAM 73.6, 73.7, 73.8, 73.9 (5 560 shells). All of this material was collected originally as a single sample.

Type locality. Beermullah, Western Australia. Lat. $31^{\circ} 11' S$, long. $115^{\circ} 42' E$. "Benalong" bore at northern part of Swan Location 5261, about 0.5 km east of Location 2680, ("Pin Pin"); 4.6-4.9 m below ground surface (Fig. 2).

Diagnosis. A medium-sized *Coxiella* up to 17 mm high, of somewhat variable form, elongate-conical or turritulate, with height about twice the maximum diameter. Protoconch smooth, paucispiral, either present or absent through decollation, in which case a septum is formed. Whorls convexly rounded, flattened, shouldered or carinate; sometimes cingulate above the periphery, with sutures impressed or incised. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base and occasionally entirely absent. Umbilicus present, small in juveniles, becoming wide (for the genus) in mature shells. Aperture ovate to quadrate, according to the degree of carination; often with persistent yellow-brown pigmentation within. Shells white externally.

Description of holotype. Shell of medium size, elongate-conical, of 7.8 whorls in a height of 9.6 mm, maximum diameter 5.5 mm. Apex intact, protoconch smooth, paucispiral; spire whorls convexly rounded, the last whorl slightly flattened, sutures impressed. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base. Umbilicus open, small. Aperture ovate, oblique and continuous, the columellar lip everted; faintly yellow-brown within. Shell white externally.

Observations. Of the described species of *Coxiella*, (Macpherson 1957), the fossil species is closest in general shell proportions to *C. pyrrhostoma* (Cox), though not attaining the height of that species (17 against 20 mm). Other similarities are the presence of contrasting pigmentation within the aperture and the spiral striae. Some rugose, shouldered or cingulate shells of *roeae* recall specimens of *C. glauerti* Macpherson from the Esperance-Israelite Bay district. Examination of a range of specimens from that area collected since Macpherson's revision of the genus suggests to the writer that *glauerti* may be no more than a localised gerontic form of *pyrrhostoma*.

C. roeae differs markedly from *pyrrhostoma* and most other species of *Coxiella* in the relatively late onset of decollation and also in the limited extent to which this is usually manifest. This is shown among the fossils by the presence of a substantial proportion of mature shells having either intact or very slightly decollate apices. In *pyrrhostoma* by contrast, decollation appears to occur early in growth when the shell is 4-5 mm high and recurs subsequently a number of times. Juvenile, non-decollate shells of *pyrrhostoma* have a subcylindrical form in contrast to the ovate-conical form of young *roeae*. Occasional shells of *roeae* exhibit a more extensive decollation, comparable to that of extant species. Carination of the whorls in a proportion of shells distinguishes *roeae* from all other congeners. The new species is considerably more variable in shell characters than any other *Coxiella*; however the extreme forms are connected by intermediates and all are considered to represent a single species. The paratype series, a selection of which is illustrated (Fig. 2C-N), demonstrates this variation.

The carinate forms of *C. roeae* bear a remarkable resemblance to shells of *Pyrgula barroisi* Dautzenberg (Truncatellidae) from the Sea of Galilee, figured by Tchernov (1975, p. 156, Figs. 5, 6, 9).

The species is named after Mrs. R. Roe, who presented to the Western Australian Museum all of the material and collecting data utilised in this study.

Geographic range. The present species has been collected by Mrs. Roe from spoil from a series of bores, wells, seismic shotholes and other shallow excavations within 12 km to the south and east of the type locality and from a surface outcrop on the eastern side of Beermullah Lake some 8.5 km to the east. The positions

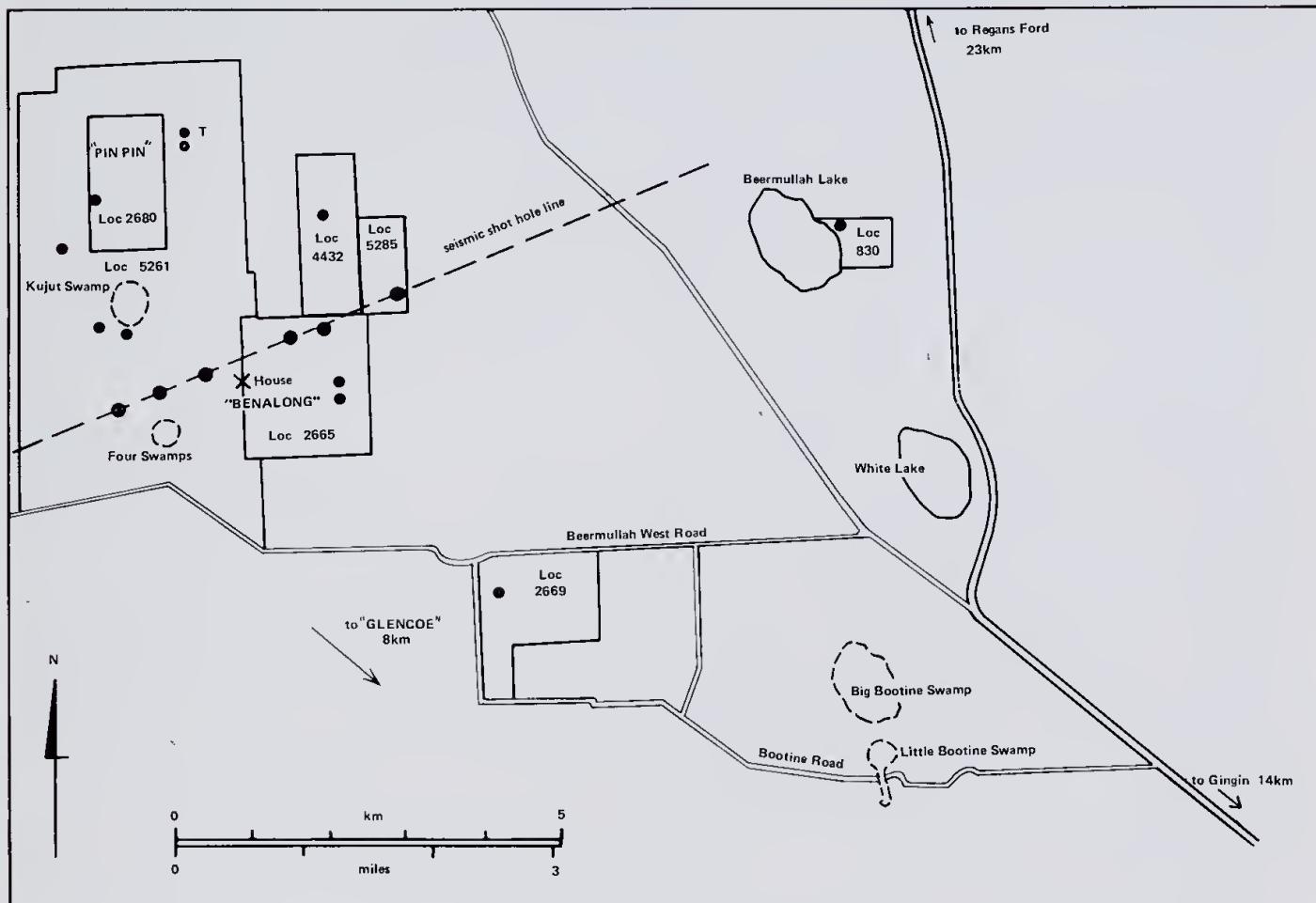


Figure 2.—Beermullah district. *Coxieilla roeae* localities. Type locality T.

of these localities are shown in Fig. 2; the greatest depth sampled was 13.7 m below the ground surface. Hosking and Greave (1936, p. 106) report "hard compact limestone containing small mollusc shells of presumably Tertiary age" from near "Glencoe" homestead, Beermullah. This property, now known as "Mirilla", lies about 8 km southeast of known occurrences of *C. roeae* and may contain an extension of the same *Coxieilla* beds. The data suggest that one or more extensive lakes may have occupied the area at the time of deposition. The presence of occasional associated fossil shells of the pond snail genera *Physastra* and *Gyraulus* (e.g. WAM 73.10, 71.984) with *C. roeae* indicates that these water bodies were more likely to have been fresh rather than saline at the time of deposition.

Stratigraphic range. The precise age of the present material cannot as yet be determined but marine mollusc shells (WAM 73.98-104, 73.106-7) from a bore on Swan Location 2680 ("Pin Pin", Fig. 2), close to the type locality of *C. roeae* but from between 27.4-36.6 m below the ground surface are, in the writer's view, of probable Pliocene age. If so, then the overlying lacustrine beds containing *C. roeae* were probably laid down during the Pleistocene. Apart from late Quaternary deposits around Lake Eyre, South Australia, containing fossils of the

extant *C. gilesi* (Angas) (Ludbrook 1956; King 1956), little has been established of the geologic history of the genus.

Subclass Euthyneura
Order Stylommatophora
Superfamily Bulimulacea
Family Bulimulidae

Genus *Bothriembryon* Pilsbry, 1894.

Bothriembryon Pilsbry, 1894. *Nautilus* 8:35-36.
Bothriembryon Pilsbry; Kendrick and Wilson, 1975.
Rec. West. Aust. Mus. 3:312 (with synonymy and redescription).

Type species (by original designation): *Bulimus melo* (Quoy and Gaimard) = *Helix melo* Quoy and Gaimard.

***Bothriembryon gardneri* sp. nov.**
(Fig. 4, A-E)

Material. Holotype WAM 70.1603a. Paratypes WAM 70.1603b and c, 2 shells; 66.794a and b, 2 shells embedded in a laminar piece of brown calcarenite; 66.798a, h and w, 3 shells; FMNH 194694/3, 3 shells. Other reference material WAM 70.1603d to p, 13 topotypes; 66.795, 1 shell in hard, brown calcarenite; 66.796, 2 shells in hard, brown calcarenite; 66.797, 2 shells in a large, laminar piece of brown calcarenite; 66.798, 18 complete and 31 fragmentary shells; 62.196, 1 shell in brown calcarenite; 62.197, 1

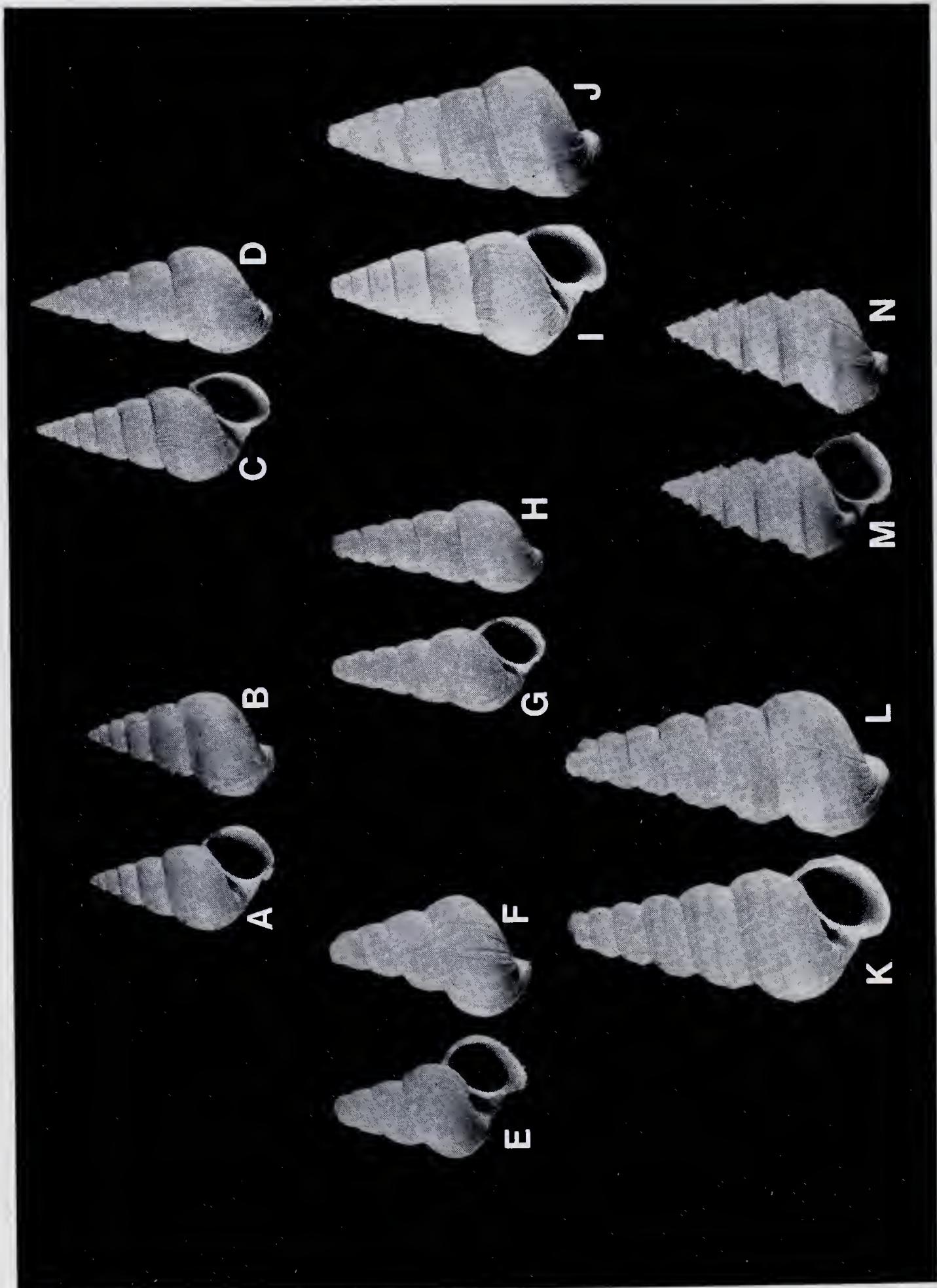


Figure 3.—*Coxiella roeae* sp. nov. A, B.—Holotype, WAM 73.4. C.-N.—Paratypes, 73.5 a-f. All \times 3.

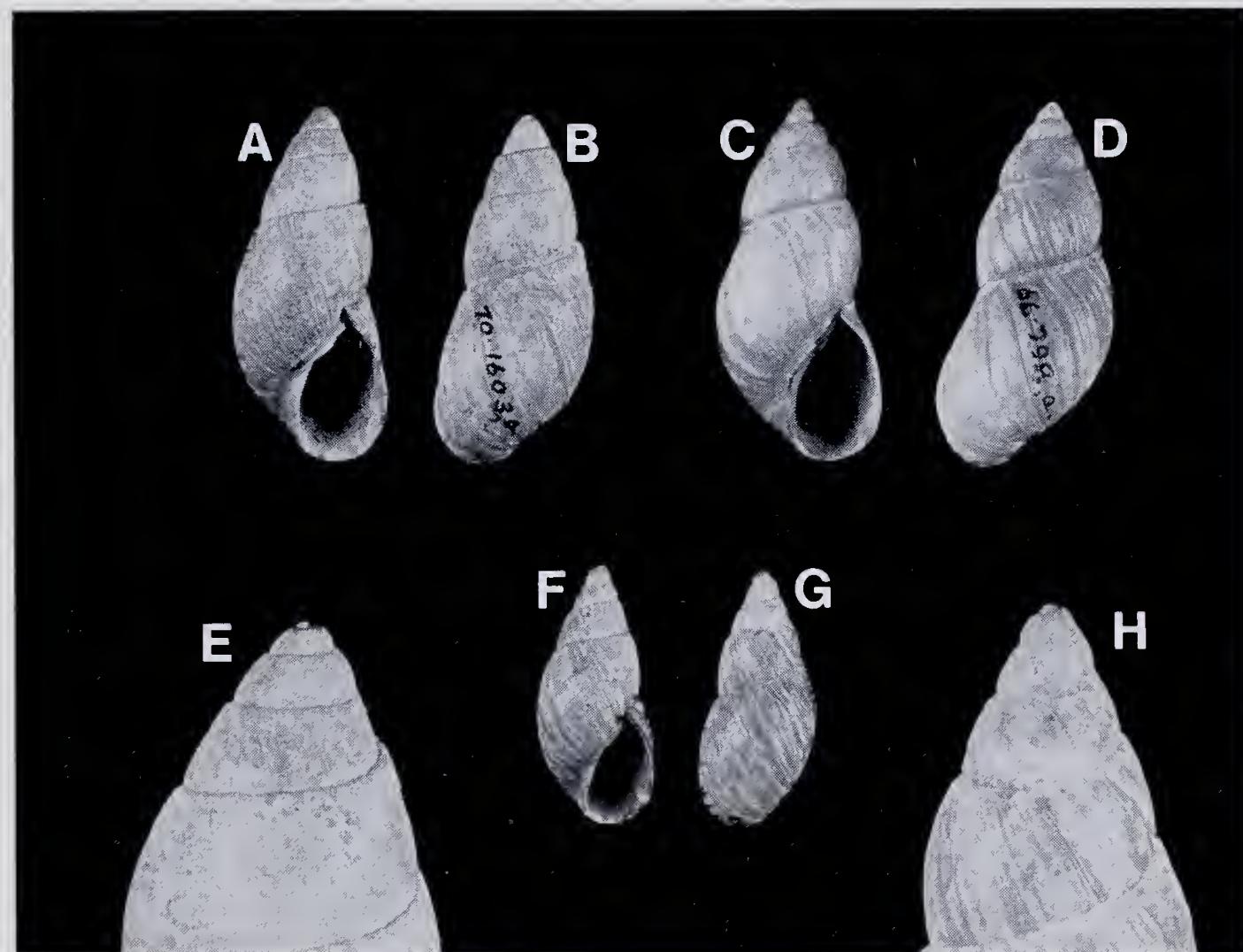


Figure 4.—*Bothriembryon gardneri* sp. nov. A, B, E.—Holotype, WAM 70.1603a C.-D.—Paratype 66.798a. *Bothriembryon consors* sp. nov. F.-H.—Holotype, 72.421a E. and H. x 3; all others x 1.

shell filled with brown calcarenite; 65.33, 2 shells; 65.34, 3 shells; 65.480, 1 shell; 70.900, 10 shells; 72.420, 32 shells; 73.253, 1 deformed shell, probably of this species; 73.254, 1 shell; 75.860, 2 shells; 9881, 2 shells in brown calcarenite: FMNH 182298, 7 shells.

Type locality. Point d'Entrecasteaux, Western Australia. Shallow quarry on crest of low ridge of calcarenite on north side of track from Windy Harbour to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecasteaux lighthouse. Lat. 34°49'14"S, long. 116°00'52"E (Fig. 5).

Diagnosis. A large, robust *Bothriembryon*, elongate-ovate, up to 45 mm high, with a height usually greater than twice the maximum diameter and spire height more than half the total height. Whorls convex, about 5.7 in a height of 40 mm, sculpture of strong, colabral growth rugae, generally without spiral granulation. Protoconch of 2.1-2.3 slightly convex whorls, dome-shaped; sculpture fine, mainly reticulate over the first 1.5 whorls and tending to become axially aligned or wrinkled over the abapical portion, where weak axial rugae may also dev-

elop. Traces of whitish axial flames are sometimes apparent on the abapical portion of the protoconch.

Description of holotype. Shell large, robust, of 6 whorls in a height of 43.5 mm, maximum diameter 19.5 mm, height of spire 24 mm. Whorls convex, suture impressed and lightly crenulated; sculpture of colabral growth rugae, concentrated below the suture; spiral sculpture absent. Umbilical fissure small. Parietal callus thick, columella concave, thick and reflected. Protoconch dome-shaped, of 2.1 whorls, bearing a fine axially-reticulate sculpture, which becomes progressively more axial on the abapical portion, where weak axial rugae, anticipating the teleoconch sculpture, also appear. The cavity of the shell contains a friable, cream calcarenite.

Observations. Of the described species of *Bothriembryon* from Western Australia (Iredale 1939), *B. gardneri* most resembles *B. fuscus* Thiele from the south coastal Karri forests between Torbay and Walpole. In the shape, size and sculpture of the protoconch, the two species are quite similar; furthermore in each a weak axial flame pattern can be detected occasionally

on the abapical extremity of the protoconch. The two species differ essentially in features of the teleoconch. The fossil species has a rather more elongate shell than *fuscus*; though attaining a slightly greater height than the living species (45 mm against 43 mm), *gardneri* does not reach the maximum width of *fuscus* (19.5 mm against 21 mm). The spire height of mature shells of *gardneri* invariably exceeds the aperture height, whereas in *fuscus* these dimensions are about equal, as Iredale noted. In details of the sculpture, the two species also differ. Axial growth rugae are much stronger in *gardneri* and spiral granulation is generally absent; traces of this feature may be detected under magnification on an occasional shell. Fine spiral granulation and (sometimes) striation ornament the spire whorls of *fuscus*. These occur on the shell proper and are not mere periostracal features. A Field Museum paratype from the Pt. d'Entrecasteaux cliff near the lighthouse shows traces of a wide, axial flame pattern on the teleoconch, such as occurs on some shells of *fuscus*.

This comparison of *B. gardneri* and *B. fuscus* shows that the two share a range of common characters and probably are closely related. Possibly the former stands in an ancestral position to the latter. If so, then the direction of morphologic change has tended toward a shorter, more ovate shell with fine spiral granulation in lieu of strong axial rugae. The presumably non-adaptive protoconch characters have remained unaltered over this time.

Fossil snails associated with *B. gardneri* include two congenors, one of which, *B. consors* sp. nov., is described below, as well as species of *Paralaoma*, and *Magilaoma* (Punctidae), *Pernagera* and one other charopid (Charopidae) and an undescribed assimineid (A. Solem, pers. comm., Sept. 1976). This assemblage suggests a humid, well-vegetated, probably forested environment at Point d'Entrecasteaux at the time of deposition, in contrast to the exposed coastal heath that presently characterises the area.

The species is named after Mr. G. Gardner of Northcliffe, who introduced the author to the type locality and assisted in the collection of the type material.

Geographic range. *Bothriembryon gardneri* is known only from the type and adjacent localities at Point d'Entrecasteaux, within 4 km of the lighthouse (Fig. 5). The material has been collected from natural and man-made exposures of fossil soils occurring on and beneath the surface of an elevated ridge of aeolian calcarenite, now truncated by a prominent sea cliff.

Stratigraphic range. No direct evidence of age for the calcarenite deposits at Point d'Entrecasteaux is available but, by analogy with similar formations in south-western Australia (Lowry 1967), a Pleistocene age is assumed. The uppermost fossil soil, containing abundant land snail shells, is generally well lithified and underlies a thin, brown, surface (possible deflated) quartz sand. A Pleistocene age for the fossils appears probable.

Bothriembryon consors sp. nov.

(Fig. 4, F, H)

Material. Holotype WAM 72.421a. Paratypes WAM 72.421b to e, j and k, 6 shells; 70.901a and b, 2 shells; 70.1602d, 1 shell. Other reference material WAM 70.1602a to c, e to g, i to m, o to q, 14 shells.

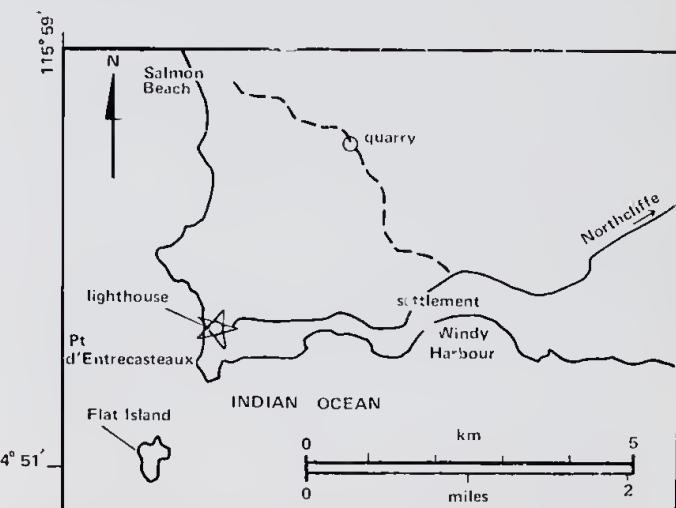


Figure 5.—Point d'Entrecasteaux and Windy Harbour. Quarry is type locality of *Bothriembryon gardneri* and *B. consors*.

Type locality. Windy Harbour, Western Australia. Shallow quarry NE of lighthouse beside track to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecasteaux lighthouse. Lat. 34° 49' 14" S, long. 116° 00' 52" E (Fig. 5). This is the same place as the type locality of *Bothriembryon gardneri*, cited above.

Diagnosis. A medium-sized, robust *Bothriembryon*, elongate, up to 32 mm high, with a height about 2.1 times the maximum diameter; spire height slightly more than half the total height. Whorls gently convex, about 5.5 in a height of 30 mm; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Traces of narrow, brown and white axial striping are visible on some shells. Protoconch of 1.9 to 2.2 whorls, elevated, somewhat tumid, sculpture finely punctate with or without a weak axial alignment and becoming very finely axially wrinkled on the abapical extremity; pale axial flames present on the second whorl.

Description of holotype. Shell medium-sized, elongate, of 5.3 whorls in a height of 29.9 mm, maximum diameter 13.8 mm, height of spire 16.0 mm. Whorls gently convex, suture impressed and finely crenulated; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Columella slightly concave and reflected over a minute umbilical fissure. The teleoconch retains faded, narrow, brown and white axial striping. Protoconch elevated, slightly tumid, of 2.1 convex whorls bearing fine reticulate-punctate sculpture, which becomes axially wrinkled near the

abapical extremity; pale axial flames present on the second whorl. The cavity of the shell contains a friable, cream calcarenite.

Observations. From the combination of an attenuate shell, axially striped and with weak spiral granulation and a protoconch patterned with axial flames, it appears that the affinities of *Bothriembryon consors* lie with a group of species from south coastal districts typified by *B. kingii* (Gray). Shells of this general form occur from the vicinity of East Mt Barren westward to the Meerup River some 20 km north of Point d'Entrecasteaux, being represented by the species *maxwelli* Kobelt, *jacksoni* Iredale, *notatus* Iredale as well as *kingii*. The field relationships and precise differentiation of these species await clarification but examination of a range of recently collected material in the Western Australian Museum suggests that there is much intergradation in shell characters. Whether they represent one wide-ranging, variable species or several has yet to be demonstrated conclusively, but despite a generalised resemblance, the fossil species, *consors*, does not closely correspond to shells from any part of this series. Such similarities as can be seen are more noticeable with the attenuate shells that occur from Albany eastward and least of all with the wide, ovate shells that characterise the western end of the series.

In the ratio of height to maximum diameter, *consors* resembles shells of the type population of *B. kingii* from Albany, but differs in other characters. The fossil attains 5.5 whorls in a height of 30 mm, whereas *kingii* reaches only about 22 mm for this degree of coiling. The protoconch of *consors* is larger, more tumid, more finely sculptured and shows less axial alignment of the sculpture than typical *kingii*. Shells of *B. jacksoni* from the Walpole-Nornalup National Park are relatively wide with a height: maximum diameter ratio of 1.8:1, attaining 5.5 whorls in 27 mm; protoconch sculpture tends to be closer to that of *consors* than *kingii* but the teleoconch characters diverge markedly. Throughout the entire modern *kingii* series, the shells tend to be thin and fragile, even where obtained from calcareous coastal soils. By contrast, the shells of *consors* are all robust, some exceptionally so. This contrast between the two species applies to specimens from similar substrates and may represent more than a simple edaphic response. The differences in shell characters between *consors* and the modern *kingii* series (*sensu lato*) indicate that the group has undergone some morphologic divergence during the Quaternary. This may have been greater in the western part of the range, with the development of a wider, ovate form of shell. An overall trend within the group seems to have been the evolution of a relatively thin shell.

B. gardneri and *B. consors* contrast strongly in characters of the teleoconch. The former and larger species has about 5.7 whorls in a height of 40 mm, the latter about 5.5 spirally granose whorls in only 30 mm. The protoconchs of the two species differ in the number of whorls, degree of elevation, sculpture and pattern.

Geographic range. *Bothriembryon consors* is known only from the type and adjacent localities at Windy Harbour (= Point d'Entrecasteaux) within 4 km of the lighthouse (Fig. 5). The localities parallel those for *B. gardneri*, both species occurring together in the same fossil soils at Point d'Entrecasteaux. The name *consors* alludes to this association.

Stratigraphic range. As for *B. gardneri*, probably Pleistocene.

***Bothriembryon douglasi* sp. nov.**

(Fig. 6, A-E)

Material. Holotype WAM 66.1036a. Paratypes WAM 66.1036b, c, 2 shells; 68.1434c, d, g, j and o, 5 shells. Other reference material, WAM 66.1036d to f, 3 shells; 68.1434a, b, e, f, h, i, k to n, 10 shells.

Type locality. Sea cliff at the Carrarang-Tamala boundary fence, Edel Land, Shark Bay, Western Australia. Lat. $26^{\circ} 32' 26''$ S, long. $113^{\circ} 26' 42''$ E; from within the top 7.5 m of the cliff (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, up to 35 mm high, height about 1.7 times the maximum diameter and attaining about 5.5 whorls in a height of 27 mm. Spire about half the total height or less; sculpture of fine, irregular growth lines crossed above the periphery by weak spiral granulation. Columella thin; umbilicus small, open. Protoconch bluntly rounded, of 2.1 to 2.4 wide, convex whorls, sculptured with fine, close irregular axial wrinkles. Protoconch apparently of one colour, slightly darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, of 6.0 whorls in a height of 34.2 mm, maximum diameter 19.6 mm, height of spire 17.0 mm. Whorls convex, suture impressed and edged with a weak groove, base evenly rounded; sculpture of growth lines crossed above the periphery with fine, spiral granulation. Columella thin, reflected, partly obscured by matrix; umbilicus small. Protoconch of 2.1 whorls, rather worn but retaining traces of fine, close axial wrinkling; slightly darker than the teleoconch. The type is a dull-white, somewhat worn shell, cracked on the spire and lacking small sections of the outer layer in several places; the exterior carries some thin, pale-brown calcareous and the cavity is filled with a hard, pale-brown quartzose calcarenite.

Observations. In the form of the teleoconch and the sculpture and deeper shading of the protoconch, only one species, *B. distinctus* Iredale from the Balladonia district (Iredale 1939) shows any significant resemblance to *B. douglasi*. The similarity is less obvious with larger fossils, such as the type of *douglasi*, but more so with smaller shells, such as those from the "Zuytdorp" locality (Fig. 7), which are about the same size as mature specimens of *distinctus*. Spiral granulation on the teleoconch is a little stronger in *distinctus* and there is a size difference in the protoconch; that of *douglasi* ranges from 2.1 to 2.4 whorls, *distinctus* from 1.7 to 2.1 whorls. These differences, together

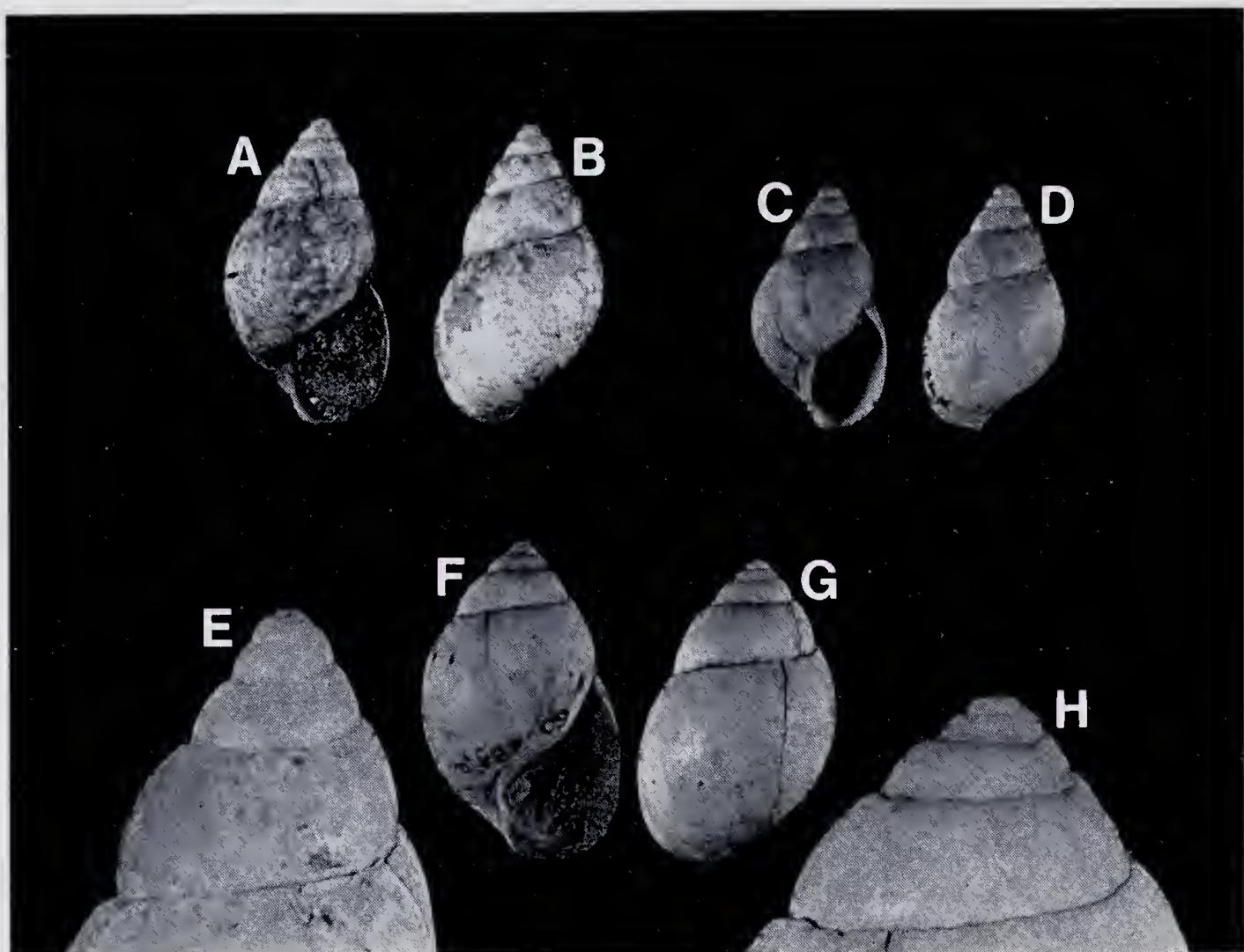


Figure 6.—*Bothriembryon douglasi* sp. nov. A.B.—Holotype, WAM 66.1036a. C.—E.—Paratype 68.1434d. *Bothriembryon ridei* sp. nov. F.H.—Holotype, 60.434a. E and H x 3; all others x 1.

with the remoteness of the two geographic ranges (over 1 000 km apart) suggest that the two species have been differentiated for an appreciable time.

At the type locality, the new species is associated with fossils of *B. costulatus* (Lamarck) (WAM 66.1037); a shell, probably also of Lamarck's species has been collected from a fossil soil at the "Zuytdorp" site (WAM 68.563) (Kendrick and Wilson 1975).

The new species is named after Mr. A. M. Douglas, who collected the specimens from the "Zuytdorp" locality, employed in this description.

Geographic range. *Bothriembryon douglasi* is known only from the type locality and from a similar position on the coastal cliffs at the site of the "Zuytdorp" wreck, 70 km further south.

Stratigraphic range. At both of the known localities, shells of *B. douglasi* occur in fossil soils similar to the Depuch Formation of the Shark Bay district (Logan *et al.* 1970). Specimens are associated with brown, quartzose, calcrenites; some from the type locality also bear

thin, hard crusts of light brown calcrete. A Pleistocene age seems probable for these lithified fossil soils.

***Bothriembryon ridei* sp. nov.**
(Fig. 6, F, H)

Material. Holotype WAM 60.434a. Paratypes WAM 60.434b, d, e, 3 shells; 66.660a, 74.531a. Other reference material WAM 60.434c, e to p, 13 shells; 65.1158, 1 shell; 66.660b to 1, 11 shells; 66.675, 1 shell; 69.1207a to d, 4 shells; 70.1869a, b, 2 shells; 74.531b to h, 7 shells.

Type locality. Western side of Dorre Island, Western Australia; limestone cliffs opposite Disaster Cove. Lat. 24° 59' 52" S, long. 113° 07' 12" E (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, ventricose, up to 40 mm high, height about 1.5 times the maximum diameter and attaining about 6 whorls in a height of 38 mm. Spire less than half the total height; sculpture of fine growth lines with weak spiral granulation present above the periphery but becoming obsolete on the last whorl. Columella thin, umbilicus small. Protoconch of 1.8 to 2.1 whorls,

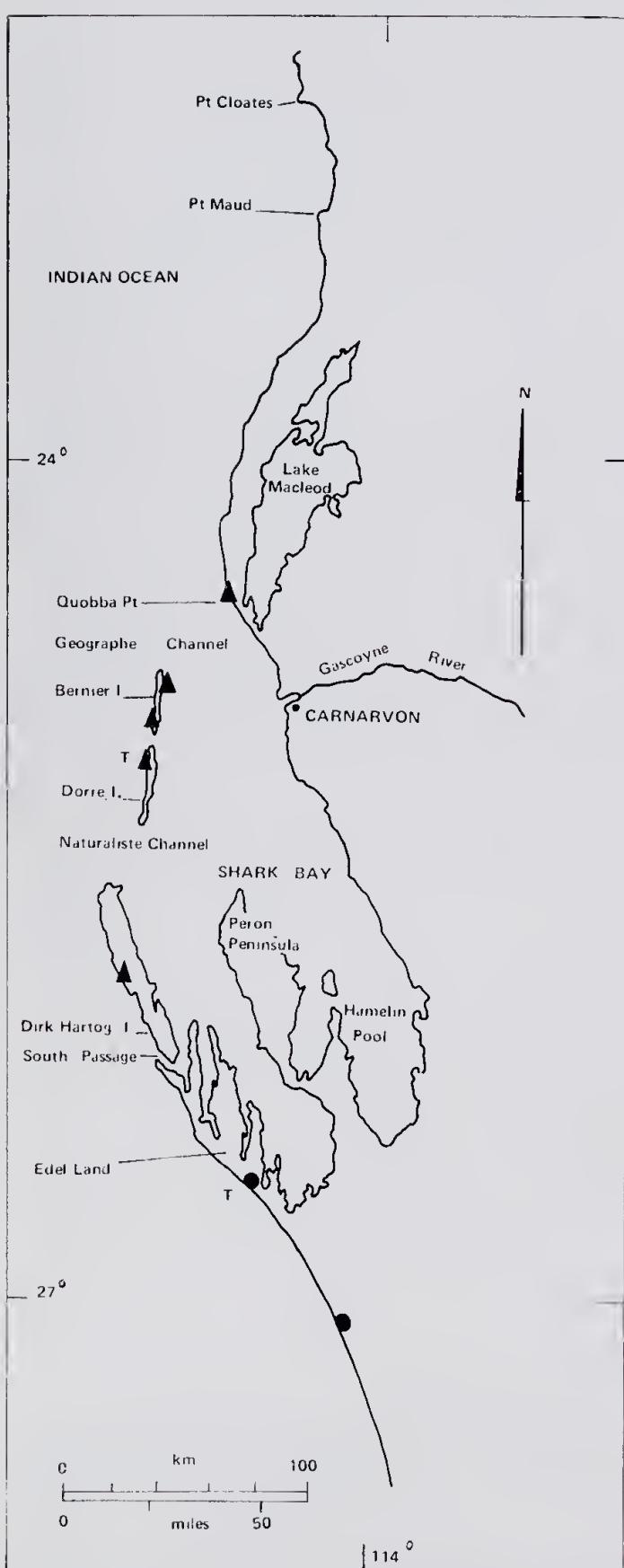


Figure 7.—Shark Bay district. *Bothriembryon douglasii* localities. ● *Bothriembryon ridei* localities. △ Type localities T.

low and wide, sculptured with axial reticulation. Protoconch apparently of one colour, tending to be darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, ventricose, of 5.9 whorls in a height of 36.3 mm, maximum diameter 22.7 mm, height of spire 16.0 mm. Whorls convex, suture impressed; sculpture of fine growth lines crossed by weak spiral granulation above the periphery and becoming obsolete on the last whorl; base evenly rounded. Columella thin, reflected; umbilicus filled with sediment. Protoconch of 2.0 whorls, low, wide, sculpture axially reticulate and strong; of one colour, slightly darker than the teleoconch. Like all the material to hand, the type is a dull white shell lacking other indication of the original colour. It is cracked in several places and part of the outer lip is missing. The cavity is filled with brown calcrete.

Observations. In form and size, *B. ridei* most resembles shells of *B. dux* (Pfeiffer), from the south coast region of Western Australia between about Ongerup and Caiguna. The new species however has a more ventricose shell, on which the spiral granulation is stronger and does not attain the height of the other (41 mm compared with 55 mm for *dux*). The protoconchs of the two species are of similar size but that of *ridei* exhibits a stronger axial component in the sculpture, best exemplified by paratype 60.434e.

The new species is named after Dr W. D. L. Ride, who, whilst Director of the Western Australian Museum, collected the type series and other material of this species.

Geographic range. Occurrences of shells of the present species at the type locality are discussed by Ride (1962, p. 24, 25, pl. 11). Additional occurrences are: Western side of Dirk Hartog Island, 32 km north of the homestead, apparently weathered from the cliff; Bernier Island, eastern coast near Wedge Rock and western coast opposite Red Cliff Point; Quobba Point near "The Blowhole".

Stratigraphic range. The report of Ride (1962) and field data recorded on labels accompanying the above material indicate that *B. ridei* occurs in fossil soils resembling those of the Depuch Formation, overlying the Tamala Eolianite. (Logan *et al.*, 1970). All specimens to hand are associated either with a dense, brown calcrete or indurated quartzose calcarenite. A Pleistocene age seems probable.

Late Quaternary climate in the Shark Bay district.

A comparison of modern and (what is known of) fossil land snail distributions in the Shark Bay district reveals some apparent contrasts which deserve consideration. Assuming that *B. douglasi* and *B. ridei* were broadly contemporaneous, it would appear that, at some as yet undefined stage of the Pleistocene, three species of *Bothriembryon*, all relatively large-shelled, inhabited the district; *ridei* occurred across western and northern Shark Bay and *douglasi* occupied the Edel Land coast (Fig. 7). The

distributions of these two species seem to have been allopatric. The third species, *costulatus*, which is extant (Kendrick and Wilson 1975), coexisted with both fossil species but the shells tended to be larger than modern specimens. The largest known example of *costulatus* (WAM 66.1037g, 6.2 whorls in a height of 30.1 mm) is a fossil from the type locality of *douglasi*. The extinction of two of these species and the size-reduction of the third presumably resulted from adverse environmental change, probably increased aridity. Whether this size-reduction applied generally to *costulatus* throughout its range, or featured local extinction and subsequent replacement by selected morphs of reduced size from outside the immediate area, remains speculative. The latter hypothesis is supported by the presence of distinctive, large-shelled populations of *costulatus* inhabiting the littoral fringe between Point Cloates and Point Maud. A shell of this form, from near the northern end of the species' range, was illustrated by Kendrick and Wilson (1975, Pl. IV, Fig. 11).

The Camaenidae, which incorporates the Chloritidae, Xanthomelontidae and Rhagadidae of Iredale (1939), are the principal family of land snails in arid Western Australia from Shark Bay northward, being particularly well developed in the Kimberley region (Wilson and

Smith 1975). At least four species represent the family in the Shark Bay district; one in particular, *Rhagada torulus* (Ferussac), is common on Bernier and Dorre Island and also occurs on Dirk Hartog Island and at Quobba and elsewhere on the mainland coast. Species of *Angasella* and *Plectorhagada* occur along the southern and south-eastern littoral and hinterland, while a *Plectorhagada* is present on Dorre Island. This group of snails is currently being studied by Dr A. Solem. Camaenid records are rare in west-coastal districts south of about latitude 27°, the peripheral occurrences in this region being *Angasella abstans* in the lower Murchison and Greenough districts (Iredale 1939 and G.W.K. unpublished notes). *A. abstans* appears to be a relict species with a strongly disjunct distribution, isolated from the main occurrences of the family. It may represent an earlier Pleistocene camaenid incursion into the northern fringe of the humid south-west. The family is absent from the south-western corner of the State, where *Bothriembryon* dominates the land-snail fauna.

No camaenid fossils have been found in association with either *B. douglasi* or *B. ridei*, despite the abundance of modern specimens, notably those of *Rhagada torulus*, at most of the known localities of the latter species (*ridei*). The few fossil records of camaenids from the

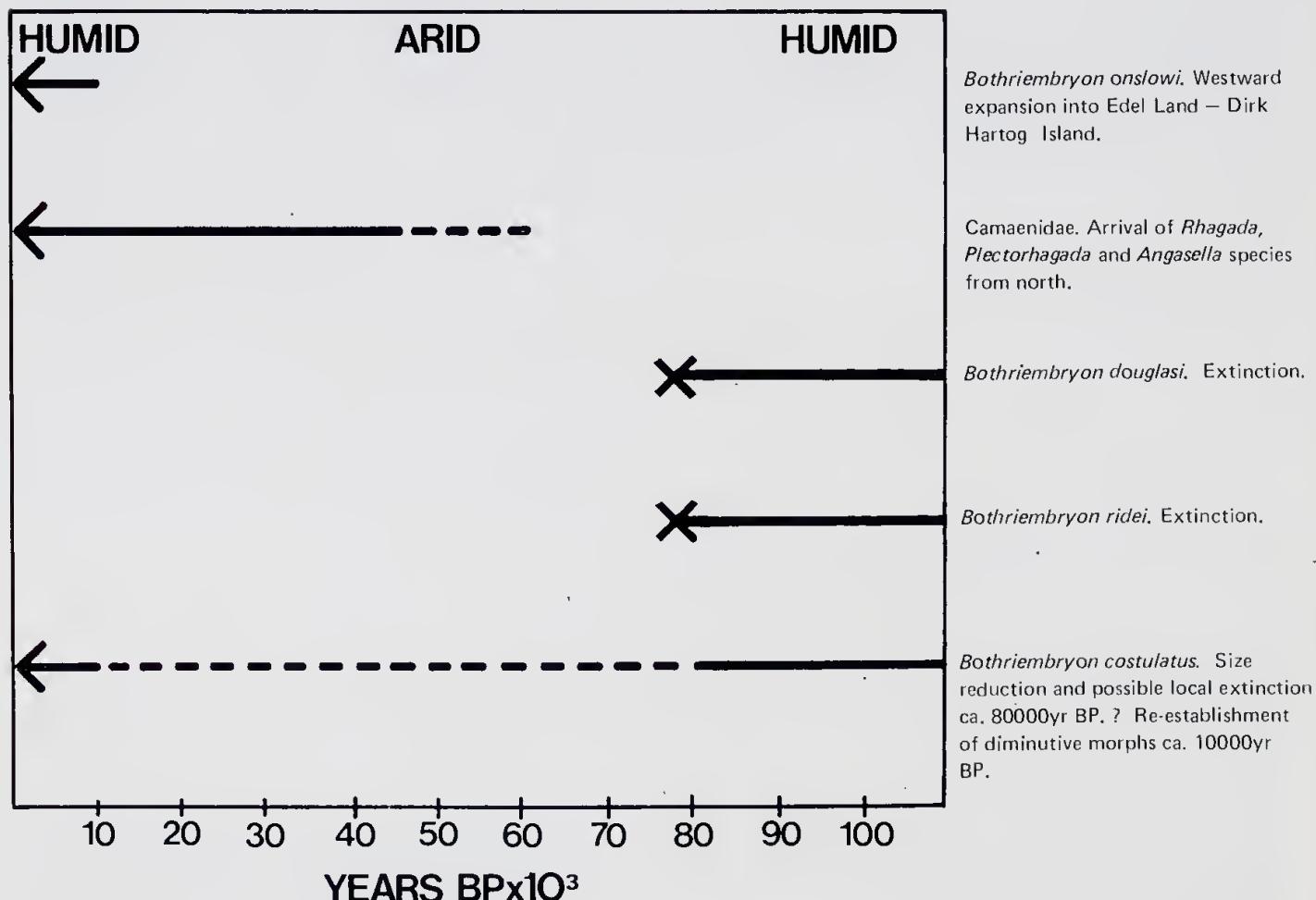


Figure 8.—Conjectural late Quaternary history of *Bothriembryon* and camaenid species in the Shark Bay District.

Shark Bay district (WAM 66.807, 73.85, 73.87) all appear to be of very recent geologic age. Significantly, all are associated with the diminutive, modern form of *Bothriembryon costulatus*, for which Iredale (1939) employed the name *B. minor* Pilsbry (Kendrick and Wilson 1975).

The evidence available from modern and fossil records suggests that the camaenid snails reached the Shark Bay district at some time after the extinction of *B. douglasi* and *B. ridei*. The demise of these two species and the size-reduction of *B. costulatus* are seen as consequences of an environmental change toward greater aridity. It is assumed that the camaenids, being pre-adapted to the drier conditions prevailing in northern areas, would have been favoured by any such change and would have extended their ranges southward and westward into the Shark Bay area. It is noteworthy that camaenids closely related to Shark Bay species are at present living in the country between the Gascoyne River and Cape Range; these may represent the original stocks from which the Shark Bay camaenid populations originated.

The timing of these events cannot yet be established precisely but some inferences can be drawn from the distribution data. Camaenid populations on Bernier and Dorre Islands have been isolated from the mainland since the submergence of the Naturaliste and Geographe Channels during the Flandrian transgression of the sea, some 8 000 year ago (Morner 1971, p. 76). The bathymetry of South Passage between Dirk Hartog Island and the mainland indicates that severance of this island probably occurred a little later. Prior to this, the mainland connections of the Shark Bay "islands" would have been continuous for the entire duration of the last major glacio-eustatic regression of the sea, corresponding to the Wurm-Weichselian glaciation of northern Europe. During this period of global cooling, which became fully assertive from about 80 000 year ago (Broecker and van Donk 1970, Emiliani 1972), sea level fell more than 100 m below its present position (van Andel *et al.* 1967). The camaenid occupation of the Shark Bay district, in particular of the western islands, probably occurred during this time. If so, it may be assumed tentatively that the extinction of *Bothriembryon douglasi* and *B. ridei* marked a transition from (relatively) humid to arid conditions beginning around 80 000 year ago (Fig. 8).

Evidence in support of relative aridity in low and middle latitudes accompanying the reduced global temperatures of the last major glaciation of the Late Pleistocene has been advanced from studies in northern and eastern Australia (van Andel *et al.* 1967; Bowler and Hamada 1971; Dodson 1975), in south-east Asia (Verstappen 1974), the equatorial Pacific (Quinn 1971), tropical South America (van der Hammen 1972) and, in a review of all continents by Williams (1975), indicating a general convergence of views in this direction. Differences between modern and fossil distributions of land snails in the Shark Bay district are consistent with such an interpretation.

Still to be considered is the history of *B. onslowi* (Cox), the second extant species of *Bothriembryon* in the Shark Bay district (Kendrick and Wilson 1975). Fossils to hand are few (WAM 66.278, 66.658, 66.668, 71.225), all being derived from modern soil profiles of young geologic age. Associated fossils include the diminutive, modern form of *B. costulatus* but, as yet, no camaenids. The distribution of *onslowi* around southern Shark Bay, in Edel Land, on Peron Peninsula and Dirk Hartog Island (but not on Bernier or Dorre Islands) suggests that it entered the westernmost part of this range at a time when Dirk Hartog Island was joined to the mainland but when Bernier and Dorre Islands were not. As noted above, this would have been some time after 8 000 year ago. The living colours of *B. onslowi* are shades of a rather intense brown, matching the strongly coloured soils of Peron Peninsula and the south-eastern hinterland of Hamelin Pool. Well-developed cryptic coloration such as this supports the view that the species has had a relatively long association with areas of deeply coloured soils and a more recent presence in Edel Land and Dirk Hartog Island, where soils are pallid.

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Thallus variation in *Hormophysa triquetra* (C. Ag.) Kuetz. (Fucales, Phaeophyta) in oceanic and estuarine habitats

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Abstract

Hormophysa triquetra (C. Ag.) Kuetz. is one of the few fucoid algae which occur in Australian estuaries. There is a gradient of form variation between oceanic and estuarine environments. The morphological differences result from reduced cell enlargement and cell division in the estuarine compared with oceanic forms. However the pattern of growth and differentiation is the same in all forms so that delimitation of taxonomic sub-groups is not appropriate at this time.

Introduction

Several fucoid algae, including species of *Ascophyllum*, *Fucus*, *Hormosira* and *Pelvetia* penetrate into brackish waters, estuaries or salt marshes from rocky ocean shorelines in Europe, North America and New Zealand (Berquist 1959, Chapman 1976, Gibb 1967, South and Hill 1970). In these non-oceanic habitats the algae tend to have narrow fronds, few vesicles, profuse branching, no holdfast and no sexual reproduction. Low salinity has been suggested as the primary cause of these form changes, although Brinkhuis (1976) and Brinkhuis and Jones (1976) show that salt marsh ecads of *Ascophyllum* are the result of tidal emergence combined with high light and high temperatures. In addition, Moss (1971) suggests that the pattern of growth in *Ascophyllum* is irreversibly changed when vegetative regeneration of thalli occurs. In Australia however, the distributions and forms of fucoids in estuaries have not been documented or studied in relation to the environmental factors controlling growth in these habitats.

The wide form variation of *Hormophysa triquetra* (C. Ag.) Kuetzing has resulted in nomenclatural and taxonomic problems, but these have been resolved by Papenfuss (1967) and Womersley (1967). Some of these variations probably are estuarine forms of the species, but this distinction has not been made. Studies by Johnson (1967), Mairh and Krishnamurthy (1970) and Papenfuss (1967) have reported only on the vegetative and reproductive anatomy of the oceanic form of *H. triquetra*. The present study compares the vegetative morphological features of oceanic and estuarine forms of *H. triquetra* in Western Australia.

Material and methods

Material of *Hormophysa triquetra* was collected from the Western Australian coastline and voucher specimens were placed in the Herbarium of the University of Western Australia (UWA). Pieces of thalli from the extremes of the morphological ranges of estuarine (Peel Inlet) and oceanic (Cottesloe reef) environments were fixed in 6% formalin seawater or modified Karpechenko's solution. The tissue pieces were paraffin embedded. Transverse serial sections (4-9 μ m) were stained with haematoxylin and mounted in Euparal. The morphologies of apical, mature and vesiculate tissue of oceanic and estuarine forms were compared by measuring tissue and cell (anticlinal and periclinal) dimensions, and by calculating the areas of the vesicular cavities. 160 cells were measured in each of 6 different thalli.

Results

Morphological variation

Although *Hormophysa triquetra* is a perennial species, it is vegetatively dormant and the fronds are denuded in winter. Growth occurs in spring and summer.

Oceanic forms: These forms occur in intertidal pools and in upper sublittoral areas of the limestone reef platforms of the southwestern Australian coast between Shark Bay (24°52'S; 113°39'E) and Fremantle (32°03'S; 115°45'E). The thallus (Fig. 1A) has triquetrous, twisted fleshy fronds with dentate, winged corners and embedded vesicles. Often, well developed lateral branches are difficult to distinguish from the main axis, resulting in a bushy habit. At north-

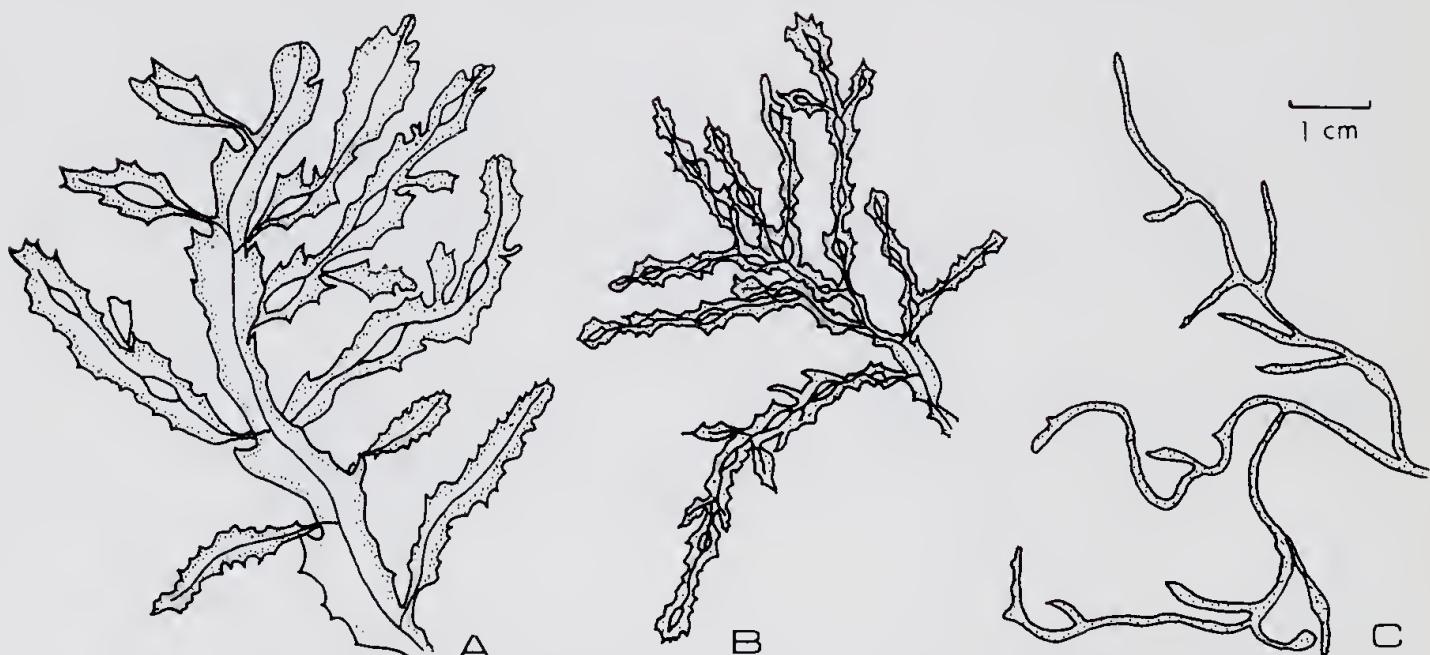


Figure 1.—A.—Portion of southern oceanic form of *Hormophysa triquetra* UWA-A1315. B.—Portion of northern oceanic form. UWA-A32. C.—Portion of estuarine form. UWA-A271.

erly locations, less fleshy specimens have been collected (Fig. 1B). Typical oceanic specimens are UWA-A1302, UWA-A1304, UWA-A1308, UWA-A1313 and UWA-A1315.

Estuarine forms: In the Swan River Estuary ($32^{\circ}03'S$; $115^{\circ}50'E$) and Peel Inlet ($32^{\circ}35'S$; $115^{\circ}43'E$), the alga grows subtidally to about 1.2 m depth. The thalli are usually attached by a holdfast to limestone rubble or to empty bivalve shells. In the most reduced forms, only portions of the lower thallus anchor the alga in the sandy substrate, or thalli without holdfasts are intertwined with the fronds of another estuarine fucoid, *Caulocystis uvifera*.

The morphology ranges from oceanic forms through reduced wing and narrow frond forms, to reduced spindly almost evesiculate forms. In the latter (Fig. 1C), frond parts near the apex are typically triquetrous, but with a tendency to become rounded lower in the thallus. The spindly forms have intertwining laterals and have a diffuse, entangled form. Typical estuarine specimens are UWA-A271, UWA-A372, UWA-A1037, UWA-A1291, UWA-A1295, UWA-A1298 and UWA-A1299.

Apical morphology

Cell divisions of the meristoderm and cortical layers built out from the faces of the tapered, triangular apical cell results in a triangular apex outline. The structure around the apical cell varies with habitat. Estuarine forms have three simple "horns" of tissue corresponding with the corners of the thallus outline. Thalli from the ocean reefs (Fig. 2A) have elaborate, tapering horns curved over the apical depression. The horns eventually contribute to the dentate wings of the mature thallus margin.

The spiral twisting of the fronds is initiated at the apex (Fig. 2B) because cells are cut off sequentially and slightly obliquely from the

apical cell. The spiral branching pattern from the corners of the triquetrous axis results from the successive initiation of lateral initials from the faces of the main apical cell. In oceanic forms (Fig. 2C), a wing of tissue overlies the entire young lateral branch. The basic spiral, monopodial growth pattern is the same in all forms of *Hormophysa triquetra*.

Mature frond and vesicle morphology

In both vesiculate and non-vesiculate areas of the mature fronds the oceanic form has larger cortical cells than the estuarine form (Fig. 3), although the dimensions of the meristoderm cells are similar in both forms. Conceptacular cavities occur in the oceanic form, but none occur in the most reduced of the estuarine forms.

Vesticles occur at irregular intervals along the fronds of both forms, but the estuarine forms have fewer vesicles. Increased cell division in the thallus surface layers ruptures the medulla and part of the inner cortex to form the vesicles cavity (Fig. 2D). The area of the vesicular cavities in the oceanic form ($\bar{x} 2.46 \text{ mm}^2$) is twice that of the vesicular cavities in the estuarine form ($\bar{x} 1.21 \text{ mm}^2$). The width of the vesicular cortex in the oceanic form ($\bar{x} 0.283 \text{ mm}$) is considerably thinner than in non-vesiculate areas of the thallus ($\bar{x} 0.388 \text{ mm}$), in contrast to the vesicular cortex of the estuarine form ($\bar{x} 0.199 \text{ mm}$) which is thicker than the non-vesicular cortex ($\bar{x} 0.153 \text{ mm}$). In both forms the inner cortex is distorted tangentially, and particularly in the oceanic form there is also rupture and loss of inner cortex cells. The

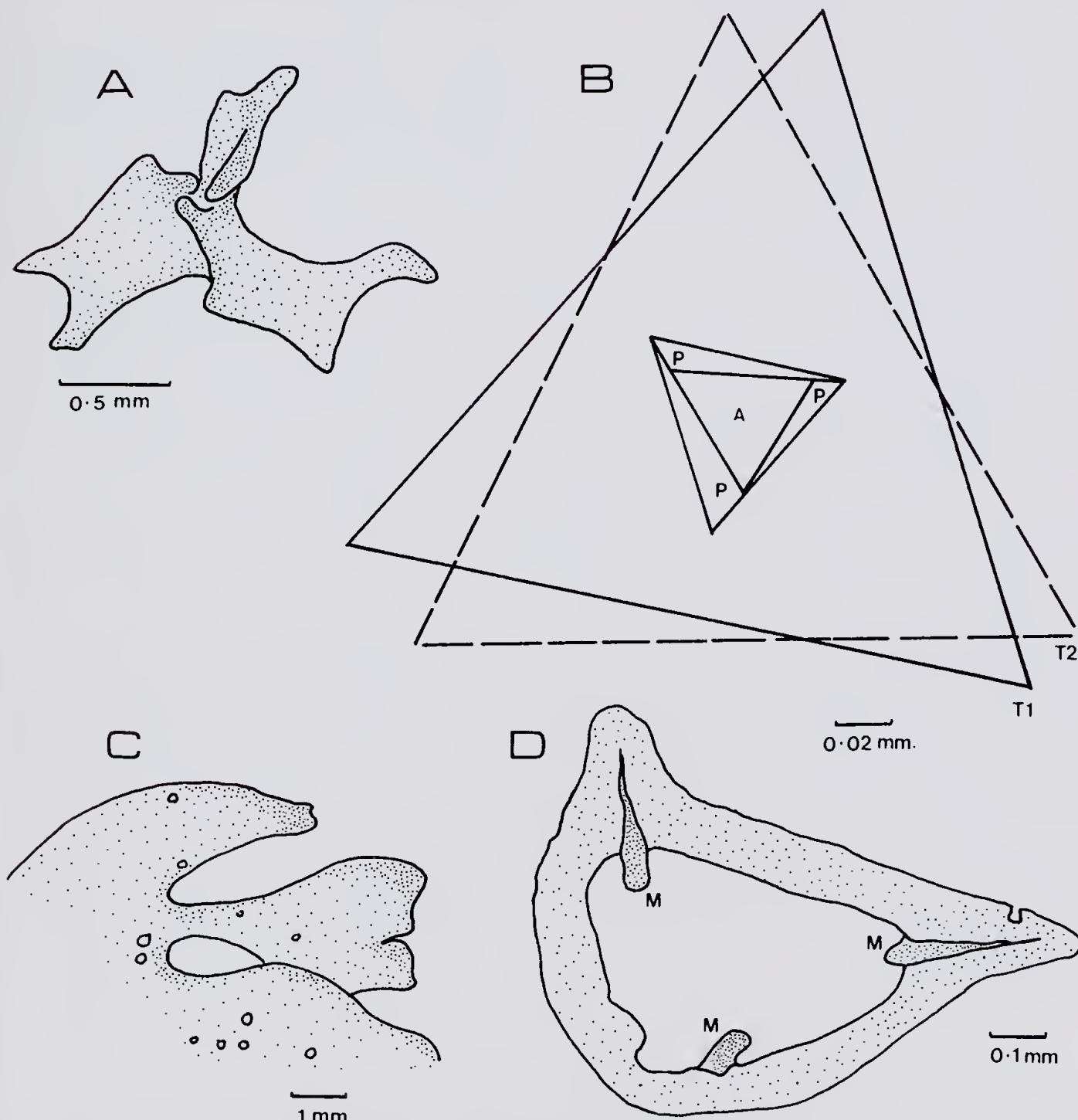


Figure 2.—A.—Top view of oceanic thallus apex of *Hormophysa triquetra* showing twisted horns over apical depression. B.—Diagrammatic outline of spiral apical growth pattern. A, apical cell; P, primary segments of apical cell division; T1 and T2, successive thallus outlines. C.—Oceanic form lateral branch apex with wing of parent thallus. D.—Transverse section of vesicle in estuarine form. M, remnant strands of medulla.

meristoderm and outer cortex cells have the same shape and size in both vesicular and non-vesicular areas since it is cell division in these tissues which forms the vesicles.

Discussion

The form variation of *Hormophysa triquetra* between oceanic and estuarine environments follows the same trend as reported for other fucoid species in similar environments. Perhaps

the same environmental factors cause similar types of morphological responses. As with other fucoids, the form variation of *H. triquetra* is a graded response suggesting that the factors controlling differentiation and form are quantitative rather than qualitative.

The morphological differences in *Ascophyllum* are attributed by Moss (1971) to fewer meristoderm cell divisions in reduced forms. In *Hormophysa triquetra* estuarine form, there are not

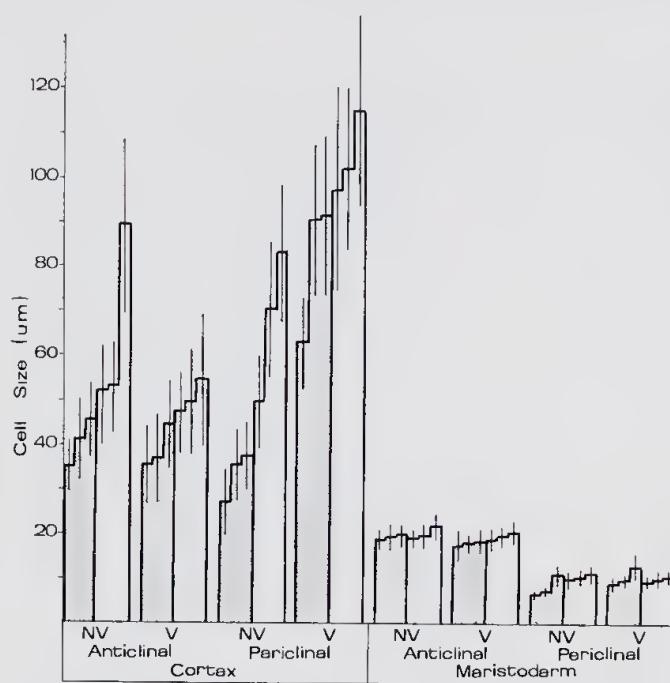


Figure 3.—Cell dimensions in vesiculate and non-vesiculate frond areas of three estuarine (shaded) and three oceanic thalli of *Hormophysa triquetra*. Anticinal and pericinal indicate directions of cell measurement. V, vesiculate; NV, non-vesiculate. Standard deviation bars are shown.

only fewer meristoderm cell divisions as evidenced by the narrower frond and vesicle areas, but also smaller cortical cells. Although vesicle volumes were not compared because this study was based upon transverse sections of material, observations of longitudinal sections suggest that the above conclusions are applicable to this dimension as well. That is, the estuarine form differs from the oceanic form in its reduced cell enlargement and cell division capacities.

As for the taxonomic significance of the form variation in *Hormophysa triquetra*, there are several considerations. Firstly, the basic spiral growth pattern from a triangular apical cell, the pattern of initiation of laterals, and the

pattern of vesicle formation are the same in all forms. Secondly there are transition forms between the morphological extremes. Therefore there seems little merit in formalizing varieties or ecads of *H. triquetra* at this time, particularly without the support of eco-physiological data. Studies of variation in *Ascophyllum* by Brinkhuis and Jones (1976) and Brinkhuis, Temple and Jones (1976) suggest the directions for further study of *H. triquetra*.

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